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Effect of mulch application in combination with NPK fertilizer in cowpea (*Vigna unguiculata* (L.) Walp.; Leguminosae) on two key pests, *Maruca vitrata* F. (Lepidoptera: Pyralidae) and *Megalurothrips sjostedti* Trybom (Thysanoptera: Thripidae), and their respective parasitoids

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To my parents.

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Summary

Mulching is a traditional means used by African farmers to preserve soils from physical and nutritional degradation. Despite many research efforts on various crops described in the literature, no clear evidence exists whether mulch may also be used successfully to control pests. This study aimed to assess the effect of organic soil cover (mulch) in combination with NPK fertilizer on two key pests of cowpea (*Vigna unguiculata* (L.) Walp.; Leguminosae), the legume pod borer *Maruca vitrata* F. (syn. *M. testulalis* [Geyer]) (Lepidoptera: Pyralidae) and the flower thrips, *Megalurothrips sjostedti* Trybom (Thysanoptera: Thripidae), inclusive of their parasitoids. Exact trials were carried out in three regions of Benin, West Africa, from March 1995 to August 1997, covering five consecutive rainy seasons. Trials were performed using repeated measurements that allowed multivariate data analysis as repeated measures in mixed models.

This study focused on several aspects, such as plant physiology, soil properties, climate (e.g., precipitation, temperature) as well as habitat structure (wild host plants), all of which were assumed to have a strong influence, direct or indirect, on pest dynamics and abundance. Considering the plant's phenology as major factor in determining pests' appearance, data on plant development represented by number of nodes, flowers, and pods were collected periodically. Flowers were sampled in parallel to monitor the abundance of both pests. Mulch affected plant growth marginally only. This was ascribed to the short-term conditions of the early-yielding cowpea variety, which left most of the beneficial mulch effects underexploited by the time the plant was ready to be harvested. Applied chemical fertilizer showed strong impact on vegetative growth and, in part, on flower set, but the plants were forced into vegetative overgrowth to the detriment of reproductive parts. If coinciding with early reproductive organs of cowpea, thrips led to considerable flower shedding and subsequent loss in pod set.

The evaluation of insect counts from the flower samples revealed that mulch had no direct effect on pest abundance. The few events of slight increase were ascribed to improved soil humidity, which resulted in slightly higher flower numbers thus attracting more pests. NPK fertilizer increased flower numbers in most cases as an indirect positive effect, which led to higher pest abundance. The change in metabolism of the plant due to NPK application amplified pest abundance for both larvae and adults. The better nutrient supply may have been attractive for adults of *M. sjostedti* thus leading to more oviposition, and also ameliorated conditions for the successful development of larvae. The masking effect of early thrips attacks on the presence of *M. vitrata* was confirmed. Low precipitation during the early reproductive phase of cowpea enhanced this effect, whereas higher precipitation delayed the build-up of thrips populations in favor of *M. vitrata*, the larvae of which found more favorable feeding conditions.

Eggs and living larvae of *M. vitrata* and larvae of *M. sjostedti* were collected periodically and reared for studies on parasitism. Death rate analysis was used to assess mortalities due to mainly three braconid parasitoids belonging to the order of hymenoptera, *Dolichogenidea* sp., *Phanerotoma leucobasis* Kriechbaumer, and *Braunsia kriegeri* Enderlein, which represented the dominant species of a guild on larvae of *M. vitrata*. *Ceranisus menes* Walker (Hymenoptera: Eulophidae) was the only parasitoid found on *M. sjostedti*. The presence of suitable alternative host plant communities in the vicinity of cowpea enhanced parasitoid activity resulting in increased mortalities of pest larvae. Regional and seasonal differences in parasitism levels were explained mainly by the species composition of wild hosts and the presence or absence of alternative feeding and oviposition sites available for antagonists. The change of metabolism in plants by NPK application positively influenced parasitization rates. A negative density-dependent parasitism rate was observed. Increasing abundance of both pest larvae resulted in decreasing relative parasitization successes by parasitoids. Depending on the population age structure, mortalities differed considerably due to parasitoids' affinity for specific instars. Isolated cases, where parasitoids appeared to benefit from a shelter effect by mulch, gave rise to the conclusion that the secondary importance of mulch did not offer an appropriate tool for pest control.

Pods of selected plants were harvested periodically and assessed for damage of *M. vitrata*. Measures such as pod number, weight per pod, relative pod and grain damage were investigated and estimates were made of the yield losses that were caused by *M. vitrata*. Pod and grain damage was influenced principally by larval abundance in flowers and pods in combination with number of pods per plant. The presence of late instars in flowers suggested that migration into pods is not necessary for the completion of larval development. The ratio of late to early instars assisted in explaining increased grain damage through prolonged presence of larvae in pods. Prolonged precipitation delayed the ripening process and thus led to increased grain damage over time as the suitability of tissue deteriorated more slowly. Pod weight, which is correlated with seed number and size as well as pod length, helped interpreting grain damage in relation to pod size. Total yield losses caused by *M. vitrata* on pods did not reach substantial levels and were of low economic importance, mostly remaining below 10%.

Final yields of cowpea were measured and related to preceding pest abundance and physiological properties of plants. Selected plants per plot were harvested entirely. Dried pods were counted, weighed, and husked, and grains were weighed for final yields. Flower numbers per plant were considered the basic measure for determining cowpea yield, while pest abundance, soil properties, and natural flower shedding further decided on the number of pods finally set given the initial number of flowers. Pests were identified as the most important cause of yield reduction or failure. Whereas NPK led to vegetative overgrowth of the plants to the detriment of reproductive organs, it ameliorated plants' vigor, which improved their tolerance to higher thrips abundance. Mulch had no influence. Due to the multi-level interactions, it was difficult to predict seed yield of cowpea on the basis of preceding pest attacks only.

Both pests *M. vitrata* and *M. sjostedti* maintain a permanent population throughout the year without diapause while switching among a wide range of different host plants. Flowers per potential host species of both pests were collected periodically in the vicinity of cowpea fields. Insect counts from flowers in the adjacent cowpea fields served as comparison. Pest monitoring in flowers of wild host plants continued throughout the year. *M. vitrata* was rarely encountered in wild hosts. Results for *M. sjostedti* showed that pest abundance was generally low when no cowpea was present. With the onset of first organs suitable for adults of *M. sjostedti* to feed and oviposit on, adult numbers in nearby wild hosts increased rapidly. Scarcity of feeding sites following increased pest pressure in cowpea explained a subsequent migration to wild hosts. The response of larval numbers in alternative hosts was weak and indicated a higher oviposition preference for cowpea, which led to often very high populations. Aging cowpea, which ceased flowering and changed its metabolism, led to decreasing thrips populations in both cowpea and wild hosts. This indicated that abundance together with qualitative aspects of resources determined the size of the population. Parasitism on larvae of *M. vitrata* was generally higher in cowpea compared with wild hosts. A higher diversity of parasitoid species in cowpea and their cumulative success across species was held responsible. Larvae of *M. sjostedti* showed overall low parasitization rates, which were comparatively higher in wild host plants. The limited recognition of cowpea as host of *M. sjostedti* and a probably higher affinity for other thrips' species were discussed.

The results of this approach indicated that none of the factors under investigation dominated in terms of an overall main effect. Their interaction barely permitted clear-cut predictions. These findings led to the recommendation that direct NPK application to cowpea should be avoided since the high input costs cannot be justified. Furthermore, mulch needs to be appraised under long-term conditions, which are more likely to unfold its beneficial effects. The short-term conditions of the present study indicated that the low impact of mulch on pests and parasitoids did not furnish an appropriate tool for efficient control. Pests' populations could not be suppressed while a positive effect on parasitoids' successes was not observed, either. Regional patterns could be ascribed basically to soil properties, precipitation as well as abundance and species composition of wild host plants in the vicinity of cowpea. Whereas the soil characteristics together with precipitation exerted strong influence on cowpea growth, its resulting phenology in the framework of the availability of alternative host plants determined pests' dynamics and abundance.

Zusammenfassung

Afrikanische Bauern verwenden traditionell Pflanzenmulche, um Fruchtbarkeit und Textur von Böden zu erhalten. Viele der Literatur entnommene Studien zur Erforschung von Mulch in verschiedenen Kulturpflanzen konnten nicht eindeutig klären, ob sich organische

Bodenbedeckung auch zur Schädlingskontrolle eignet. Ziel der vorliegenden Arbeit ist die Beschreibung der Effekte von Mulch und NPK-Dünger auf die Kuhbohne *Vigna unguiculata* (L.) Walp. (Leguminosae) und ihre Schlüsselschädlinge, den Hülsenbohrer *Maruca vitrata* F. (syn. *M. testulalis* [Geyer]) und den Blütenthrips *Megalurothrips sjostedti* Trybom, sowie deren Parasitoide. In drei Regionen Benins (Westafrika) wurden Exaktversuche zwischen März 1995 und August 1997 während fünf aufeinanderfolgender Regenzeiten durchgeführt. Die Datenerhebung erfolgte nach der Methode der sogenannten Meßwiederholung und erlaubte multivariate statistische Auswertung auf der Grundlage von Zeitreihenanalysen als gemischte Modelle.

Einflußfaktoren wie Pflanzenphysiologie, Bodeneigenschaften, Klima (Niederschläge, Temperatur) sowie das angrenzende Habitat (wilde Wirtspflanzen), von deren starker direkter oder indirekter Ausprägung auf Schädlingsdynamik und -aufkommen ausgegangen werden konnte, wurden untersucht. Die Phänologie der Kuhbohne wurde als wichtigster Faktor zur Interpretation des Schädlingsaufkommens erachtet. Zu deren Messung wurden wöchentlich Nodien, Blüten und Hülsen erfaßt. Gleichzeitig wurden beide Schädlingsarten ausgezählt. Der Einfluß von Mulch auf die Phänologie der Pflanze war geringfügig. Als Hauptgrund dafür wurde die Frühreife der gepflanzten Sorte angeführt, die bereits geerntet war, wenn der zu erwartende Mulcheffekt mit Verzögerung eintraf. Chemischer Dünger beeinflußte vorwiegend die vegetative Entwicklung der Pflanzen und wirkte sich nur teilweise auf die Blütenentwicklung aus. Die Pflanze entwickelte mehr vegetative Masse, die zu Ungunsten der generativen Entwicklung ausfiel. Wenn Thripsbefall bereits in der frühen generativen Phase der Pflanze auftrat, führte dies zu starkem Blütenfall und folglich einer Reduzierung des Hülsenertrages.

Aus der Analyse der obengenannten Schädlingszahlen in Blüten ging kein direkter Einfluß von Mulch auf das Schädlingsaufkommen hervor. Die wenigen Male, bei denen eine leichte Erhöhung der Population durch Mulch festgestellt wurde, waren auf verbesserte Bodenfeuchte zurückzuführen, die eine Erhöhung der Blütenzahl und damit verbesserte Attraktivität für Schädlinge zur Folge hatte. NPK-Dünger erhöhte die Blütenzahlen und führte damit zu höheren Schädlingspopulationen. Die Düngung verursachte vermutlich zusätzlich eine Veränderung im Stoffwechsel der Pflanze mit direkter positiver Wirkung auf Larven und Adulte der Schädlinge. Während Adulte durch die verbesserte Nahrungsqualität angezogen wurden und mit erhöhter Eiablage reagierten, war die Nahrungsgrundlage der geschlüpften Larven geeigneter für eine erfolgreiche Entwicklung. Der Maskierungseffekt früh auftretenden Thripsbefalls auf die Populationsentwicklung von *M. vitrata* konnte bestätigt werden. Geringer Niederschlag während der frühen reproduktiven Phase der Kuhbohne verstärkte dieses Phänomen, wohingegen erhöhter Niederschlag zu verzögertem Thripsbefall führte und demzufolge verbesserten Entwicklungsbedingungen für *M. vitrata*.

Eier und lebende Larven von *M. vitrata* sowie Larven von *M. sjostedti* wurden wöchentlich gesammelt und im Labor zu Parasitierungsstudien gezüchtet. Nennenswerte

Mortalität war hauptsächlich auf drei Parasitoide der Hymenopteren-Familie *Braconidae* zurückzuführen, namentlich *Dolichogenidea* sp., *Phanerotoma leucobasis* Kriechbaumer und *Braunsia kriegeri* Enderlein. Die einzige aus Larven von *M. sjostedti* schlüpfende Parasitoidenart war *Ceranisus menes* Walker (Hymenoptera: Eulophidae). Wildwachsende Pflanzengemeinschaften als alternative Nahrungsquelle in der Umgebung der Kuhbohnenfelder erhöhten die Mortalitäten der Schädlingslarven durch Parasitismus. Regionale und saisonale Unterschiede in Parasitierungsraten in der Kuhbohne wurden vorwiegend durch die Spezieszusammensetzung der wilden Wirte als alternative Nahrungsquellen und Eiablageplätze für die natürlichen Gegenspieler erklärt. In Parzellen mit NPK-Düngung traten erhöhte Parasitierungsraten auf, möglicherweise hervorgerufen durch eine erhöhte Attraktivität der Pflanzen für die Parasitoide. Eine deutliche negative Dichteabhängigkeit wurde zwischen Anzahl von Schädlingslarven und den Parasitierungsraten beobachtet, wobei zunehmende Schädlingsdichten zu deren abnehmender relativer Parasitierung führten. Die Spezifität der einzelnen Parasitoidenarten für bestimmte Larvenstadien von *M. vitrata* führte zu unterschiedlichen Mortalitäten je nach Altersstruktur der Larvenpopulation. Die wenigen Fälle eines Schutzeffektes von Mulch für Parasitoide ließen den Schluß zu, daß Mulch als Mittel zur Schädlingskontrolle nicht geeignet ist.

Zufällig ausgewählte Pflanzen wurden wöchentlich geerntet und deren Hülsen auf Schaden durch Larven von *M. vitrata* untersucht. Hülsenzahlen, Gewicht pro Hülse, und relativer Hülsen- und Körnerschaden wurden ermittelt, auf deren Basis Ertragsverluste errechnet wurden. Hülsen- und Körnerschaden waren hauptsächlich eine Funktion aus Anzahl der Schädlingslarven in Blüten und Hülsen im Zusammenhang mit vorhandenen Hülsen pro Pflanze. Da späte Larvenstadien auch in Blüten gefunden wurden, kann davon ausgegangen werden, daß eine Migration in Hülsen zur erfolgreichen Vollendung des Larvenzyklus' nicht notwendig ist. Das Verhältnis früher zu späten Larvenstadien diente zur Erklärung erhöhten Körnerschadens durch verlängerte Anwesenheit früher Larvenstadien. Anhaltende Niederschläge verzögerten die Hülsenreife. Im Fall von *M. vitrata* kann Hülsenreife mit sich verschlechternder Nahrungsqualität gleichgesetzt werden. Verzögerte Hülsenreife bedeutet deshalb verlängerte Fraßtätigkeit mit der Folge höherer Schäden. Desweiteren war das Gewicht pro Hülse ausschlaggebend, da relativer Körnerschaden mit der Größe der Hülsen variiert. Die durch Larven von *M. vitrata* verursachten Ertragsverluste blieben mit Werten meist unter 10% insgesamt sehr gering.

Abschließend wurden die Erträge der Kuhbohne ermittelt. Als wichtigster bestimmender Faktor für den Hülsenertrag wurde der absolute Blütenansatz erachtet, wobei der tatsächliche Hülsenansatz durch Schädlingsbefall, Bodeneigenschaften sowie den natürlichen Blütenabwurf beeinflußt wurde. Schädlingsbefall war die Hauptursache für Ertragsverluste oder –ausfall. Während NPK-Düngung vegetatives Wachstum forcierte und generative Organe unterdrückte, wurden die Pflanzen durch gesteigerte Vitalität in die Lage versetzt, Thripsbefall besser zu kompensieren. Mulch hatte keinerlei Einfluß auf die Erträge. Durch die zugrundeliegenden

Wechselwirkungen der verschiedenen Faktoren ist es schwer möglich, Voraussagen über den zu erwartenden Ertrag alleine auf der Grundlage des Schädlingsbefalls zu treffen.

Beide Schädlinge waren ganzjährig in verschiedenen wildwachsenden Wirtspflanzen präsent. Wöchentlich wurden Blüten von all den Wirtspflanzen gesammelt, die in der direkten Umgebung der Kuhbohnenfelder angetroffen wurden, Proben von zufällig gesammelten Blüten in den Bohnenfeldern dienten als Vergleich. Larven von *M. vitrata* wurden nur selten in den wilden Wirten gefunden. In Abwesenheit der Kuhbohne blieben die Thripspopulationen in wilden Wirten auf niedrigem Niveau. Sobald die Kuhbohne Organe bildete, die zur Nahrungsaufnahme und Eiablage der Adulten geeignet waren, wurde ein rascher Anstieg der Adultenzahlen in den wilden Wirten beobachtet. Nahrungsverknappung durch steigende Populationsdichten in der Kuhbohne war der Hauptgrund der Auswanderung der Thripse in alternative Wirte. Dahingegen blieb das Niveau der Larvenzahlen in wilden Wirten überwiegend konstant und ließ den Schluß zu, daß die Eiablage und damit beträchtlicher Populationsaufbau vorwiegend in der Kuhbohne stattfand. Ausgehend von den Erhebungen in den wilden Wirten in der direkten Umgebung, kann eine großflächige Dispersion der aus der Kuhbohne auswandernden Adulten in die weitere Umgebung angenommen werden. Alternde Kuhbohnenbestände, gekennzeichnet durch eine Stoffwechselveränderung (Verlagerung von Assimilaten, speziell Stickstoffverbindungen, in reifende Hülsen) und rückläufige Blütenzahlen, führten zu abnehmendem Schädlingsbefall in der Bohne und in den wilden Wirten. Es kann davon ausgegangen werden, daß die Populationsgröße vorwiegend durch Nahrungsangebot und –qualität gesteuert wird. *M. vitrata* wurde in der Kuhbohne stärker parasitiert als in den wilden Wirten. Dies wurde mit der höheren Diversität der Parasitoide in der Kuhbohne erklärt, die zu insgesamt höheren Parasitierungserfolgen führte. Der Parasitoid von *M. sjostedti* erzielte in wilden Wirten deutlich höhere Erfolge im Vergleich zur Kuhbohne. Die begrenzte Erkennung der Kuhbohne als Wirt von *M. sjostedti* durch den Parasitoiden und dessen vermutlich bessere Affinität zu anderen Thripsspezies wurde dafür verantwortlich gemacht.

Die Ergebnisse der Versuche führten zu der Schlußfolgerung, daß direkte NPK-Düngung zur Kuhbohne vermieden werden sollte und Mulch in weiteren Studien auf seinen anzunehmenden positiven Langzeiteffekt untersucht werden sollte. Mulch konnte unter den gegebenen Kurzzeitbedingungen keine Wirkungen entfalten, die hinsichtlich einer Schädlingsbekämpfung hätten genutzt werden können, da weder negative Effekte auf die Schädlingspopulationen noch fördernde Einflüsse auf die Parasitoide beobachtet wurden. Als zentrale Größen, die zu regional starken Unterschieden führten, galten Bodeneigenschaften, Niederschlagsverteilung und die Verteilung sowie Abundanz wilder Wirte. Während die Bodenqualität im Zusammenhang mit dem Niederschlag das Pflanzenwachstum dominant beeinflußte, war die daraus resultierende Phänologie der Kuhbohne zusammen mit der Verfügbarkeit alternativer Nahrungsangebote ausschlaggebend für den Schädlingsdruck.

Résumé

Le système du mulch est un moyen traditionnel utilisé par les paysans africains pour préserver les sols des dégradations physiques et nutritionnelles. Malgré les multiples efforts de recherche sur diverses cultures telles que consignés dans la littérature, aucune étude précise ne met en relief la possibilité de l'utilisation du mulch pour le contrôle efficace des ravageurs. En fait il s'agit d'apprécier l'effet de la couverture organique du sol (mulch) en combinaison avec l'engrais NPK sur deux ravageurs clés du niébé (*Vigna unguiculata* (L.) Walp.; Leguminosae), notamment le foreur de gousses *Maruca vitrata* F. (syn. *M. testulalis* [Geyer]) (Lepidoptera: Pyralidae) et les thrips de fleurs *Megalurothrips sjostedti* Trybom (Thysanoptera: Thripidae), y compris leurs parasitoïdes. Des essais en milieu réel ont été exécutés dans trois régions du Bénin, en Afrique de l'Ouest, de Mars 1995 à Août 1997 couvrant ainsi cinq saisons de pluies consécutives. Des méthodes de mesurage en répétition ont été utilisées pour ces essais ce qui permit l'analyse des données multivariates en modèles mixtes.

Dans cette étude, l'accent a été mis sur plusieurs aspects comme la physiologie de la plante, les propriétés du sol, le climat (p.ex. précipitation, température) ainsi que la structure de l'habitat (les plantes hôtes sauvages); tous ces éléments étaient présumés avoir une forte influence, directe ou indirecte, sur la dynamique et l'abondance des ravageurs. Considérant la phénologie des plantes comme facteur principal pour déterminer l'apparition du ravageur, les données sur le développement des plantes représenté par le nombre de nœuds, de fleurs, et de gousses ont été périodiquement collectées. Parallèlement, les fleurs ont été échantillonnées pour évaluer l'abondance des deux ravageurs. Le mulch n'affectait la croissance des plantes que de façon très légère. Cette situation est imputée aux conditions de cycle court de la variété précoce de niébé qui laisse les effets bénéfiques du mulch sous exploité apparaître au moment où la plante est à même d'être récolté. L'application de l'engrais chimique a montré un impact important sur la croissance végétative et en partie sur l'apparition des fleurs. Cependant, les plantes ont été plus enclins à une surcroissance végétative au détriment des organes reproductifs. Lorsqu'ils coïncident avec les organes reproductifs précoces du niébé, les thrips conduisirent à une chute considérable des fleurs et une perte subséquente dans la formation de gousses. Les résultats de cette approche ont indiqué qu'aucun de ces facteurs ci-dessus étudiés n'a été dominant du point de vue d'effet principal majeur. C'est à peine que leurs interactions permirent de nettes prédictions.

L'évaluation du comptage d'insectes telle que décrite plus haut à partir des échantillons de fleurs, a révélé que le mulch n'avait aucun effet direct sur l'abondance des ravageurs. Les quelques cas de légère augmentation ont été attribués à l'amélioration de l'humidité du sol ce qui aboutit à un plus grand nombre de fleurs attirant ainsi plus de ravageurs. L'engrais NPK a

fait augmenter le nombre de fleurs dans la plupart des cas révélant ainsi son effet positif indirect, ce qui conduisit à une forte population du ravageur.

Le changement dans le métabolisme des plantes du fait de l'application de NPK, a amplifié l'abondance du ravageur (larves et adultes). Alors que l'approvisionnement en meilleurs éléments nutritifs auraient été attractifs aux adultes de *M. sjostedti* conduisant à plus d'oviposition, les conditions pour un développement réussi des larves ont été ainsi améliorées. L'effet masqué d'attaques précoces de thrips en présence de *M. vitrata* a été confirmé. Les faibles précipitations durant la phase précoce reproductive du niébé ont stimulé cet effet tandis que les fortes précipitations retardèrent la reconstitution des populations de thrips en faveur de *M. vitrata,* les larves de cette pyrale trouvant de bonnes conditions d'alimentation.

Les œufs et les larves vivantes de*M. vitrata* ainsi que celles de *M. sjostedti* ont été périodiquement collectés et élevés pour les études sur le parasitisme. L'analyse du taux de mortalité a été faite pour estimer les mortalités dues principalement à trois braconides appartenant à l'ordre des hyménoptères, *Dolichogenidea* sp., *Phanerotoma leucobasis* Kriechbaumer et *Braunsia kriegeri* Enderlein, représentant les espèces dominantes de la guilde des parasitoïdes des larves de *M. vitrata*. *Ceranisus menes* Walker (Hymenoptera: Eulophidae) était le seul parasitoïde trouvé sur *M. sjostedti*. La présence de communautés de plantes hôtes alternatives convenables dans les environs du champ de niébé stimula les activités des parasitoïdes ce qui conduisit à une augmentation de mortalités de larves de ravageurs. Les différences de parasitisme au niveau saisonnier et régional ont été principalement justifiés avec la composition des espèces des plantes hôtes sauvages, la présence ou non des sites alternatifs d'alimentation ou d'oviposition convenables aux ennemis naturels. Le changement du métabolisme dans les plantes dû à l'application de NPK a positivement influencé le taux de parasitisme. Un taux de parasitisme de densité dépendante négative a été observé. L'augmentation de l'abondance des larves des deux ravageurs a conduit à une diminution relative du taux de succès des parasitoï des. En fonction des structures d'âges des populations, les mortalités ont considérablement varié en raison de l'affinité des parasitoïdes vis -à-vis des stades spécifiques. Des cas isolés où les parasitoïdes ont semblé bénéficier de l'effet d'abri du mulch, donnèrent lieu à la conclusion que par rapport à son importance secondaire, le mulch n'avait pas offert un outil approprié pour le contrôle du ravageur.

Les gousses des plantes choisis ont été périodiquement récoltées en vue de l'évaluation des dommages causés par *M. vitrata*. Les paramètres tels que le nombre de gousses, le poids par gousse, les dégâts relatifs aux gousses et aux grains ont été examinés puis les pertes de rendements estimées. Les dégâts aux grains et gousses ont été principalement influencés par l'abondance des larves dans les fleurs et gousses et tributaires du nombre de gousses par plante. La présence des derniers stades larvaires dans les fleurs a montré que la migration dans la gousse n'est pas indispensable pour l'achèvement du développement larvaire. Le ratio derniers à premiers stades appuie l'explication de l'accroissement des dégâts aux grains par un séjour prolongé des larves dans les gousses. Les précipitations prolongées retardèrent le pro-

cessus de maturité et conduisirent à une augmentation des dégâts aux grains sur un long moment pendant que la suitabilité du tissu connaît une détérioration progressive. Le poids de gousses, corrélé au nombre et à la taille des grains ainsi qu'à la longueur de la gousse, a aidé à expliquer les dégâts des grains en rapport avec la taille des gousses. Les pertes totales de rendements dues à *M. vitrata* sur les gousses n'avaient pas atteint les niveaux substantiels et étaient d'importance économique faible, niveaux qui pour la plupart restent en-dessous de 10%.

Les rendements finals du niébé ont été mesurés et rattachés à l'abondance du ravageur et aux propriétés physiologiques des plantes. Des plantes choisis par parcelle ont été entièrement récoltés. Les gousses sèches ont été comptées, pesées, battues et les grains pesés. Le nombre de fleurs par plante a été considéré comme mesure de base déterminant le rendement du niébé, alors que l'abondance du ravageur, les propriétés du sol et plus tard la chute naturelle des fleurs régirent pour un nombre initial de fleurs données, le nombre de gousses qui finalement est formé. Les ravageurs ont été identifiés comme la cause la plus importante de réduction ou de perte de rendement. Alors que l'engrais NPK a conduit à une croissance végétative poussée des plantes au détriment des organes reproductifs, il a de même favorisé la vigueur des plantes ce qui améliora leur tolérance vis-à-vis de fortes apparitions de thrips. Le mulch n'avait aucune influence. Du fait des interactions à niveau multiple, il a été difficile de prédire les rendements en grains du niébé sur la seule base des attaques du ravageur.

Les deux ravageurs *M. vitrata* et *M. sjostedti* maintiennent une population permanente sans diapause durant toute l'année, se déplaçant au sein de la large gamme variée de plantes hôtes. Les fleurs de chaque espèce d'hôte potentiel de ces ravageurs ont été périodiquement collectées dans les environs des champs du niébé. Le comptage des insectes à l'intérieur des fleurs provenant des champs adjacents du niébé servit de base de comparaison. Le suivi du ravageur à l'intérieur des fleurs des plantes hôtes sauvages est poursuivi pendant toute l'année. *M. vitrata* a été rarement rencontré dans les hôtes sauvages. Les résultats de *M. sjostedti* ont montré que l'abondance du ravageur était généralement faible en cas d'absence du niébé. Mais avec l'apparition des premiers organes appropriés pour l'alimentation et l'oviposition des adultes, le nombre de ceux-ci au niveau des hôtes sauvages connut une rapide croissance. La rareté des sites d'alimentation suivant la pression parasitaire croissante dans le niébé permit d'expliquer les migrations subséquentes dans les hôtes sauvages. Le nombre de larves dans ces hôtes était faible montrant ainsi la forte préférence du niébé comme site d'oviposition; ce qui a souvent conduit à de très fortes populations. Les vieux champs de niébé qui ont cessé de fleurir et dont le métabolisme a changé ont conduit à une baisse de population des thrips observée également dans les hôtes sauvages. Ceci indiqua que cette abondance en liaison avec les aspects qualitatifs de ressources déterminèrent la taille de la population. Le parasitisme sur les larves de *M. vitrata* a été généralement plus élevé dans le niébé que dans les hôtes sauvages. La diversité des espèces de parasitoïdes dans les champs de niébé ainsi que leur succès cum ulatif suivant les espèces est rendu responsable de ce fait. Les taux de parasitisme larvaires de

M. sjostedti ont été globalement faibles mais élevés en comparaison avec ceux observés dans les plantes hôtes sauvages. La reconnaissance limitée du niébé comme hôte de *M. sjostedti* et sa probable grande affinité vis-à-vis d'autres espèces de thrips furent discutées.

Ces résultats conduisirent à la recommandation selon laquelle l'application directe de NKP au niébé devrait être évitée puisque les coûts élevés impliqués dans cette opération ne peuvent être justifiés. De plus le mulch devrait plutôt être évalué sous les conditions à long terme qui feraient probablement ressortir ses effets bénéfiques. Les conditions à court terme de la présente étude ont indiqué que le faible impact du mulch sur les ravageurs et parasitoïdes ne fournit point un instrument approprié pour un contrôle efficace. Les populations des ravageurs ne pouvaient être réprimées du moment où l'effet positif du succès des parasitoïdes n'a pas été non plus observé.

Des modèles suivant les régions pourraient être établis en se basant sur les propriétés du sol, les précipitations, l'abondance et la composition des espèces de plantes hôtes sauvages aux environs du champ du niébé. Alors que les caractéristiques du sol mises ensemble avec les précipitations ont exercé une forte influence sur la croissance du niébé, la phénologie qui en résulte dans le contexte de disponibilité des plantes hôtes alternatives a déterminé l'abondance et la dynamique des ravageurs.

List of abbreviations

x^{d}	number to the power of d: detransformed mean from least squares means procedure (LSMeans) in SAS
x^{*}	*F*– or c^2–value marked with one star: significant at $0.05 > P \geq 0.01$
x^{**}	*F*– or c^2–value marked with two stars: significant at $P < 0.01$
$x^{[l]}/x^{[q]}/x^{[c]}$	*F*– or c^2–value marked with $^{[l]}/^{[q]}/^{[c]}$: $^{[l]}$ = contrast on the linear trend (first order polynomial), $^{[q]}$ = contrast on the quadratic trend (second order polynomial), $^{[c]}$ = contrast on the cubic trend (third order polynomial)
DAP	Days after planting (sowing)
Mean ± SEM	Mean followed by its standard error (standard error of the mean)
NPK^{-}, NPK^{+}	NPK^{-} refers to plots that did not receive NPK fertilizer; they are also referred to as non-fertilized plots, blank plots or zero plots. NPK^{+} refers to plots fertilized with NPK.
Control	plots without mulch
Senna	plots with *Senna siamea* mulch
Imperata	plots with *Imperata cylindrica* mulch
Neem	plots with *Azadirachta indica* mulch

Map of Benin with research sites

Source: Central Intelligence Agency (CIA) from Perry-Castañeda Library Map Collection

Introduction

Cowpea (*Vigna unguiculata* (L.) Walp.; Leguminosae), also known as black-eyed bean or southern pea (Singh & van Emden 1979; Singh 1990), is a widely distributed plant, cultivated mainly in the tropics and subtropics (Alghali 1991a). It is thought to have originated from the southern regions of Africa, whereas its domestication occurred in the savanna regions of West Africa (Rachie & Roberts 1974; Steele & Mehra 1980; Summerfield & Roberts 1983; Summerfield et al. 1983; Vaillancourt & Weeden 1992; Padulosi & Ng 1997). It is an important source of protein in many developing countries (Gethi & Khaemba 1985; Alghali 1991a,b).

A considerable range of pests causes different types of damage to cowpea. At least 85 species have been recorded (Raheja 1976), and it is probable that these are the major limiting factors in cowpea production (Summerfield & Roberts 1983). Nine of them are considered important pests in the world (Jackai 1995). Of these, the legume pod borer, *Maruca vitrata* F. (syn. *M. testulalis* [Geyer]) (Lepidoptera: Pyralidae) and the flower thrips, *Megalurothrips sjostedti* Trybom (Thysanoptera: Thripidae), are thought to be key pests, the control of which is a major problem all over Africa (Wien & Tayo 1979; Atachi & Ahohuendo 1989; Singh 1990). The yield losses caused by both are remarkable: *M. vitrata* may cause up to 60% damage to the crop, whereas attacks by *M. sjostedti* may lead to complete loss of flower production (Taylor 1964; Singh & van Emden 1979; van de Klashorst & Tamò 1995). In many locations their pest status is difficult to determine. Damage by *M. sjostedti* often masks the real importance of subsequent pests, e.g., *M. vitrata* (Jackai & Singh 1991). However, the range of damage by the two pests encompasses the majority of the plant's life-cycle, commencing with young tender shoots and continuing to the late reproductive phase, when mature pods are attacked (*M. vitrata*).

Several insecticides (e.g., methomyl, cypermethrin, endosulfan, dimethoate) have proven efficient in control of both pests (Singh & Allen 1980; Price et al. 1983; Mensah 1988; Ivbijaro & Bolaji 1990; Afun et al. 1991; Jagginavar et al. 1991). Thus, the control of pests by insecticides is not a technical problem. Although significant increases in yields have been demonstrated (Muller & Sellshop 1954; Booker 1965; Ebong 1965; Ojehomon 1970; Cardona & Karel 1990; Afun et al. 1991; Jackai, pers. comm.), and available alternatives are generally less effective than these chemicals (Jackai 1995), adoption rates are still low. Since smallholder subsistence farmers can barely afford the high and permanently rising input costs (Radwanski & Wickens 1981) to attain chemical pest control, cheaper, but more toxic alternatives are often chosen (Tamò et al. 1997). Although chemical control is a highly effective means, it is a dubious long-term solution and cannot be a sustainable alternative to ecological biological protocols. In order to avoid the deleterious side-effects of chemical products, a sound pest manage-

ment strategy minimizing or, preferably, eliminating the use of insecticide application must be developed (Singh 1990).

Taylor (1968) performed trials with *Bacillus thuringiensis* Berliner, which showed promising results against the larvae of *M. vitrata,* indicating its potential for integrated pest control. However, *B. thuringiensis* is unstable when exposed to ultra violet rays and might be of limited efficiency in tropical environments (Zebitz, pers. comm.). The as yet unsolved problem in integrated pest management (IPM) is the significant difference between African subsistence-farming systems (e.g., mixed cropping systems of small plot size) and those designed for large-scale monocultures in industrialized countries. In addition, lack of information on occurrence, behavior and peak activities of pests in the respective countries hinders more rapid progress (Singh 1990).

Breeding efforts on host plant resistance were made with regard to various defense mechanisms (Marfo 1985; Salifu et al. 1988a,b; Jackai & Oghiakhe 1989; Echendu & Akingbohungbe 1990; Latunde-Dada 1990; Singh 1990; Oghiakhe et al. 1991, 1993a; Ngugi et al. 1995). Screening for pod borer resistance has been performed since 1974 at the International Institute of Tropical Agriculture (IITA) with only limited progress, often as a result of non-uniform or low infestation levels (Singh 1990). Improved varieties exist where moderate resistance was incorporated. However, supplemental insecticidal protection for good yields is required, even if the amount is much less than for susceptible varieties (Singh 1990). These varieties, however, are not reliable yet in regions with high pest levels.

Cultural practices, such as protection for main crops by the associated crops, remain controversial (Tamò et al. 1997) and are far from any breakthrough in pest management in cowpea. Even if, under experimental conditions, monocultures showed higher diversity and activity of natural enemies attracted by a comparatively high prey and host population, predators and parasites appear to be more efficient in complex (polycultural) systems (Root 1973; Altieri et al. 1978). In general, pest-control strategies must be based on an understanding of the physiology of cowpea itself since this is the template for manipulation of the pest-control tactics (Singh 1990).

While host plant resistance is the first line of defense of the plant (internal approach), biological control is the most important ecological mechanism for regulating pest populations (external approach). Biological control may be defined as a naturally-occurring as well as an applied control (Huffaker & Smith 1980), the latter being of major importance for the study to be performed. Until now there has been no clear evidence of the role played by the parasites and predators of the major insect pests of cowpea, as far as the African continent is concerned. However, a number of antagonists were found on cowpea pests (Fagade 1966; Taylor 1967; Kranz et al. 1979; Okeyo-Owuor et al. 1991; Arodokoun 1996; Tamò et al. 1997). Whether these observations can be put to the advantage of the farmers is as yet uncertain and requires investigation (Singh 1990).

One aspect that has yet to be studied adequately is the use of more “natural inputs” such as plant associations or organic matter to reduce “crop stress” (Turk et al. 1980; Schoningh 1985; Daisley et al. 1988; Gupta & Rao 1989; Neuenschwander et al. 1990), which can influence, indirectly, behavioral aspects of the pest-enemy complex. Neuenschwander et al. (1990) used small amounts of mulch of cassava leaves to reduce stress of cassava plants (improving nutrient and water supply) with a significant reduction of its colonization by the cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Homoptera: Pseudococcidae). The underlying changes in the metabolism of the host subsequently affect the response of pests (Lewis 1973; Ananthakrishnan & Gopichandran 1993). The use of mulch for its direct influence, e.g., by color (Wien & Summerfield 1984), by repelling or killing insect pests, or by attracting natural enemies of the pests, has to be assessed in the following study. As examples of natural inputs with direct effects Grainge et al. (1985), Tanzubil (1991), Jackai & Oyediran (1992) and Schmutterer (1990, 1995) emphasize the properties and potential of natural pesticides from the neem tree, *Azadirachta indica* A. Juss. (Rutineae: Meliaceae), and various other plants.

Concerning the efficiency of parasitoids, Bentz et al. (1996) found a significant positive influence of applying nitrogen fertilizer on the parasitization level of one parasitoid of the whitefly *Bemisia argentifolii* Bellows & Berring (Homoptera: Aleyrodidae). Thus, two different influences on pest populations and the behavior of natural enemies are basic characteristics in the study that follows. They can be split into environment-mediated (influences from outside the plant, i.e., change of microclimate by mulch) and “host plant-mediated” (Bentz et al. 1996) (influences originated by the plant as host medium, e.g., modifying certain quality aspects within the plant).

Polyphagous pests, such as the two under study, rely on a wide range of host plants, cultivated or occurring naturally, alternating throughout the year. The sustenance of a permanent population without diapause depends principally on successful shifting among host plants (Ananthakrishnan & Gopichandran 1993; Leumann 1994; Arodokoun 1996). Thus, ecological studies should include potential breeding and feeding sites that are out of reach of agricultural cultivation.

Mulching is one of several traditional techniques on the African continent to conserve water and soil resources (Reijntnes et al. 1992; Hagmann & Murwira 1996; Hiol Hiol et al. 1996; Mangisoni & Phiri 1996; Slingerland & Masdewel 1996). Upon inquiry, farmers stated that low soil fertility, degraded soils (eroded by wind and water, encrusted), losses in soil humidity, and a general decrease of productivity could be combated by the use of organic soil cover (Slingerland & Masdewel 1996). Stigter (1984) and Müller-Sämann & Kotschi (1997) define mulch as a type of soil cover of variable thickness that would act as an interface between air and soil while modifying properties of the original soil surface. The most important effects of applied organic dry mulch, distinguishing it from inorganic mulches (Davies 1975), are a lowering of soil temperature, increase in soil humidity, protection of soil structure, dwindling of erosion, suppression of weeds, impact on soilborne micro-organisms, change in soil chemis-

try and a long-term gain of mineral nutrients (Macmillan 1952; Altieri 1987; Baldy & Stigter 1991, 1993; Müller-Sämann & Kotschi 1997). Wade & Sanchez (1983) reported a better turnover of applied chemical fertilizer in combination with mulch. Dupriez & de Leener (1983) mentioned a shelter effect for beneficial arthropods. Rising precipitation for coastal West Africa and diminishing amounts for Sahelian West Africa on the basis of long-term weather record modeling (Suplee et al. 1998), mulch might become agronomically even more important. Whereas soil humidity conservation and protection against wind erosion would apply principally for dry regions, mulch may alleviate superficial run-off and leaching of vital nutrients in the wet zones. Whether the application of soil cover would influence insect behavior through an alteration of microclimate needs further investigation.

The basic aim of this study is to investigate direct and indirect influences of organic soil cover on the pest-enemy complex. Three different types of mulch are compared with a control (no mulch), with consideration of possible effects by chemical fertilizer. A complementary task attempts the elucidation of interactions with the neighboring environment from which the pests as well as their antagonists may switch into the sites under experimentation. The extent to which the application of mulch in monocultures could approximate natural systems or more sophisticated man-made cultural techniques (e.g., intercropping), focusing on their effects on insect populations, is investigated in this study. The assessment of the mutually related patterns of these two components (mulch trials, wild growing host plants) will provide a more complete view of changing pest pressure. The following questions highlight aspects of assessing the impact of mulch and its possible effect on populations of both pests and natural enemies:

1) **Microclimate:** Mixed cropping systems such as intercropping as mix, in rows, in strips, and in relay have various influences on the pest-enemy complex (Perrin & Phillips 1978). Among the most plausible reasons is modification in microclimate (e.g., shading effect). However, these results are controversial (Jackai 1995) and depend on location, type of associated plant, and the time between the sowing dates of plant communities.

   Can mulch, with its change in microclimate, affect living conditions of pests or improve habitat requirements for natural enemies (shelter, humidity, availability of alternative prey)?

2) **Soil fertility and moisture:** Nutritional (e.g., nitrogen) and water management levels show concomitant physiological effects on plants and pest populations (Painter 1951; Southwood 1973; Scriber 1984; Bentz et al. 1996). Stress on plants may interfere with their maintenance of chemical and physiological defenses (Lewis 1973; Neuenschwander et al. 1990; Ananthakrishnan & Gopichandran 1993).

Is there any noticeable relation between the use of chemical fertilizer (NPK), organic fertilizer (mulch), and the pest-enemy complex?

3) **Insecticidal ingredients:** Azadirachtin (for example) is an allelochemical insecticide and a repellent (Schmutterer 1990, 1995) when applied as seedborne product. Although leaves of *Azadirachta indica* apparently do not contain azadirachtin, several other triterpenoids were found effective against *M. vitrata* and *M. sjostedti* when applied as an aqueous extract of the leaves (Schmutterer 1995).

Do applications of leaves of A. indica *and other plants [e.g.,* Senna siamea *(Lam.) Irwin & Barneby (Leguminosae: Caesalpiniaceae),* Imperata cylindrica *(L.) Beauv. (Gramineae: Poaceae)] show similar repellent influences (allomones) on the pest-enemy complex?*

4) **Impact on stimuli:** Plant communities show interactions of different olfactory and visual stimuli (Arthur 1962; Altieri et al. 1978; Wien & Summerfield 1984; Ananthakrishnan & Gopichandran 1993; Baldy & Stigter 1993), i.e., changes in the attractiveness of the host plant due to additional stimuli from non-host plants. Likewise, location, quality, density of resources (e.g., chlorophyll content), and habitat structure, including architecture (size, growth form), influence insect diversity and abundance (Oghiakhe et al. 1991; Jackai 1995); thrips are no exception (Ananthakrishnan & Gopichandran 1993).

Does mulch interfere with levels of stimuli emanating from the cowpea plant while causing an overlap of attraction by apparently repellent stimuli?

5) **Host plant switching:** The success of polyphagous insects is closely related to their ability to exploit the diversity of potential niches (Ananthakrishnan & Gopichandran 1993). Wild hosts serve as a vital reserve to overcome a temporary shortage of the cultivated host, the cowpea.

Are local pest densities explained by the underlying habitat structure? To what extent is the regional allocation of natural feeding refuges responsible for prevailing pest patterns, facilitating population build-up and subsequent migration?

The remarkable importance in terms of damage to cowpea by these two pests is in contrast with the apparently low efficiency of locally-available natural enemies. The pests occur on a wide range of food sources and remain widely undisturbed by local enemies.

Since its first discovery in East Africa in 1905 and the subsequent description (Trybom 1908), *M. sjostedti* has never been found elsewhere outside the African continent (Palmer 1990). Of seven species of *Megalurothrips* endemic to tropical Asia, *M. sjostedti* is the only

important pest species (Tamò et al. 1997). Tamò et al. (1997) suggest that possibly different genetic centers of pests and local enemies could be one of the reasons for its pest status in Africa. Under field conditions, parasitization levels of *M. sjostedti* by a local parasitoid, *Ceranisus menes* Walker (Hymenoptera: Eulophidae), remained in total under 1% and, in the laboratory, average rates of parasitization never exceeded 15% (Tamò et al. 1997). Predictions by simulation models (Tamò et al. 1993a) indicate that a larval mortality rate of 35% by parasitism would have a beneficial effect in the cowpea field. As is the case of *M. sjostedti*, the origin of *M. vitrata* is also uncertain (Waterhouse & Norris 1987). Its center of origin may be the Indo Malaysian region (Tamò et al. 1997). Even though a substantial number of antagonists is known from Africa, their impact as control agent against *M. vitrata* is also low.

Present research efforts have indeed indicated a potential for biological control against the two pests (Tamò et al. 1997). However, additional studies leading to the augmentation of the efficiency of natural enemies and the suppression of pest populations by modification of cultural practices (i.e., application of mulch) are necessary. This study is intended to examine both interactions between *M. vitrata* and *M. sjostedti* and their natural enemies and interactions between cultivated and wild host plants as a medium for the pest-enemy complex.

The study was conducted at the Biological Control Center for Africa (BCCA) at the International Institute of Tropical Agriculture (IITA), Cotonou. It was part of a multidisciplinary special research program, headed by the University of Hohenheim, Germany, and funded by the Deutsche Forschungsgemeinschaft (DFG).

Separate chapters are assigned to each research approach in this dissertation making them principally independent from each other. Materials and methods are described separately for each chapter. Discussions and conclusions are developed using results from all other chapters that are relevant to the respective results to be discussed. This is necessary, since this study was basically dealing with multiple interactions. Chapter 1 gives complete details on experimental sites and the research design used. This was always the same for all exercises. The type of auxiliary data and their sampling methods, which served all sampling activities, are reported. Basic points of attention provide justification for the general approach, and some theoretical reflections on the way parasitism was treated are formulated. In order to shorten the statistical methods in every chapter, the theoretical statistical background is described in detail, which fully applies for every chapter.

The plant's phenology is assessed in Chapter 2. These results are considered crucial for the following chapters. Population dynamics of the targeted pests and their interactions with the plant are outlined in Chapter 3, being compulsory for the understanding of later chapters. Chapter 4 deals with the interactions between the pests under study and their respective antagonists as controlling agent. Pod damage caused by *M. vitrata* is reported in Chapter 5 and the following yield loss estimated. Final yield of cowpea, studied in Chapter 6, encompasses

the results of preceding chapters. Chapter 7 serves as the link between population dynamics in cultivated and wild host plants in order to explain migration within a limited part of habitat. The use of a design that allows concurrent monitoring of the cultivated and several wild host plants furnishes new insight into the multitrophic interactions. Chapter 8 pulls together and discusses the conclusions and recommendations of the study. All tables and figures of relevance are compiled in a separate chapter “Tables and Figures” and are referred to in the text. The first digit of the number for each table or figure serves as indicator for the chapter to which they primarily relate. Tables are displayed in the first part of the chapter, followed by figures. The Appendix furnishes the reader with additional details on wild host plants of both pests and is a complement to Chapter 7.

1 Experimental sites, research design, and statistical approach

Experimental sites and research design

Exact trials (Rohrmoser & Wermke 1986) were performed in three regions of Benin, West Africa, to evaluate the effect of mulch on the two pests *Maruca vitrata* and *Megalurothrips sjostedti* in monocropped cowpea (local variety Kpodjiguégué) and their natural enemies. Five seasons were covered from March 1995 to August 1997. One site (on-station) was located at the IITA Station (further called IITA) on an acrisol (FAO/UNESCO 1974), Abomey-Calavi (6°25'N, 2°19'E) (15 km). The two others (on-farm) were in the villages of Tokpa/Ayou on an acrisol (6°42'N, 2°04'E) (Allada region; 55 km) and Lema on a luvisol (FAO/UNESCO 1974) (7°50'N, 2°14'E) (Dassa region; 165 km) (distances from Cotonou, as the crow flies). Since the two on-farm regions have been the targets of research activities of the university-based project for years, available infrastructure could be used and access to land was considered easy. Lema, although part of the cotton producing area towards the north, is considered to be less affected by insecticide sprays because the cotton fields are fewer and more dispersed. Thus, it was often possible to find areas without regularly treated cotton, accompanied by cowpea sprayed (unauthorized) with the same chemical. Such an environment was thought to suffer less chemical pressure. This is an important assumption for studies on insects in general, and fragile pest-antagonist interactions in particular, which are strongly influenced by environmental conditions. The seasonal migration of *M. vitrata* (Taylor 1978) as well as the changing abundance of *M. sjostedti* (Wolda 1988; Tamò, pers. comm.) on a north-south gradient suggested the location of the sites in order to contrast damage patterns along this gradient. Whereas cowpea in the coastal plains (Cotonou, Allada) is cultivated under bimodal rainfall conditions, monomodal patterns prevail in Lema.

Soils are known to be very heterogeneous and a naturally occurring gradient was not assumed. Thus, the trials were installed in a randomized complete blocks design (RCBD) (treatment size 15 x 15 m) with three replications (blocks). The purpose of randomized blocking is to increase sensitivity of treatment effects under study while accommodating spatial heterogeneity due to environmental conditions (Sokal & Rohlf 1995a; Marascuilo & Serlin 1988; Snedecor & Cochran 1989; Dutilleul 1993).

Chemical fertilizer (NPK, 14-23-14) as one factor with two levels (no application, application) was combined with mulch from two plants, *Senna siamea* (Lam.) Irwin & Barneby (Leguminosae: Caesalpiniaceae) (leaves) and *Imperata cylindrica* (L.) Beauv. (Gramineae: Poaceae) (leaves) was the second factor with three levels (no mulch, mulch 1, mulch 2). Each block of this two-factorial design therefore consisted of six combinations, in the following re-

ferred to as plots. The nutritional supply of the soils at IITA were regarded as sufficient, so fertilizer applications were expected to have no marked impact on plant growth. Hence, chemical fertilizer was not applied. Instead, the factor mulch was extended by a third plant, *Azadirachta indica* A. Juss. (Rutineae: Meliaceae) (leaves). Thus, the design on-station was a one-factorial with four levels (no mulch, mulch 1, mulch 2, mulch 3). Mulch was used in quantities of 5 t/ha dry matter, chemical fertilizer NPK (except IITA) with 234 kg/ha, i.e., 5 g/plant, equivalent to 33 kg/ha nitrogen (N), 54 kg/ha phosphorus (P), and 33 kg/ha potassium (K), i.e., 0.7 g/plant N, 1.15 g/plant P, and 0.7 g/plant K. The national standard of cotton fertilizer (NPK) was used. It was applied in higher quantities than would be necessary for legume crops especially cowpea, which is known to yield even under poor soil conditions (Duke 1983). To gain more obvious effects within this factor (Sétamou et al. 1993, 1995), the amount regarded as to be sufficient was doubled (Tamò, pers. comm.). The quantity of mulch was kept at this predefined level to allow for exchange between other, interdisciplinary, trials carried out within the same project. Planting distances between rows were 80 cm and within rows 25 cm. Plant densities per hectare ranged from 36,800 to 45,300 in Tokpa/Ayou, 42,600 to 49,600 in Lema, and 52,800 to 56,000 at IITA. The seeds were graded and sown three to a whole. Two weeks later, germinated seeds were reduced to one shoot per plant hole. Soil samples were taken (0-10, 10-60 cm, separately) weeks before the initial field preparation of each season to check principal nutrient levels as well as to control for a possible bias in plant development and impact on metabolism.

Fertilizer was distributed (application per single plant) one week after sowing, mulch (freshly cut) was dispersed two weeks after sowing. For the sites at IITA as well as in the Allada region all plant material needed could be obtained in the close surroundings. Since the distribution of *S. siamea* in the Dassa region is comparatively sparse, the whole amount of mulch from this plant had to be transported from the Allada region.

Clearing of fields as well as weeding (1-2 times per season) was done by hoe in the local manner. Ridges were prepared on-farm only; on-station the cowpea was sown directly in the unprepared soil. To avoid any interference or carryover effect of previous treatments on follow-up results (Zolman 1993), the plots were changed seasonally within the same region.

The short cycle (70 days to pod ripening) of the semi-determined, well-known, and abundantly cultivated variety allowed two growing seasons between the onset of the first cropping season and the end of the second rainy season. Five seasons were harvested successfully from March 1995 until August 1997. During these five seasons, all fields were maintained identically across seasons, regions and years. Sowing dates for individual seasons were always the same for all three regions on three consecutive days to avoid bias by sowing date between regions due to different pest pressure (Enyi 1974). All first seasons (I/95, I/96, I/97) were sown the last days of May, the second season of 1995 in mid-September, and the second season of 1996 during the first days of September. In the following, season I/95, I/96, and I/97

will be referred to as first growing seasons represented by odd roman numerals and II/95 and II/96 will be called second seasons as indicated by the even roman numerals.

For all sampling activities, a strip of roughly two meters along the border of each plot (discard area) was excluded from any type of sampling to reduce influences of adjacent treatments (plots) within the same block as well as from outside the cowpea field.

Auxiliary data and their sampling methods

Two types of data are reported in this study, main data and auxiliary data. Data like soil nutrients and texture, climatic measurements concerning precipitation and temperature, further soil humidity, germination, and finally density of plant populations were sampled to serve as auxiliary data. Main investigations are assessments of plant phenology, population dynamics, parasitism, damage, and yields, as well as sampling in alternative host plants. Auxiliary data were measured in parallel to the main data sets and were used to help explain certain patterns occurring in the main data. Some of the auxiliary data were influenced by treatments themselves, e.g., soil humidity, soil sampling after harvest, and germination. Differences that were of importance are reported separately, being the basis for discussion of main results. The methods for measuring the auxiliary data are described below, taking into account the general purpose of the data.

Soil sampling. After the fields were cleared (the soil surface structure still remained untouched), soils were sampled on each plot to obtain pre-treatment scores to be used for adjustment in case of treatment differences later on. Two different depths were probed: 0-10 cm and 10-60 cm. Five samples of 0-10 cm were drilled with a large diameter core sampler along the two diagonals of each plot and put into one transparent plastic bag (30 x 20 cm – length x width) per plot. The layer of 10-60 cm was removed with a low diameter core sampler. Three samples were taken along one diagonal per plot and put into one plastic bag of the same size. The Centre National d'Agro-Pédologie (CENAP), a national institute for soil sciences, carried out the analyses. The nutrients and measures to be taken were carbon, cation exchange capacity, potassium, magnesium, nitrogen, phosphate, and pH. For the last two seasons (II/96, I/97) the sampling procedure was repeated one week after harvest to control for changes due to cowpea cultivation and treatment effects in all plots.

Measurements of climate. Local assistants recorded daily precipitation and temperature throughout the whole period form March 1995 to August 1997. Precipitation was recorded at 8 a.m. A rain gauge was put up close to the three blocks with direct graduation in mm rainfall. Rainfall amounts, which are used per week in the analyses, are sums of the preceding week not including the respective sampling day. Minimum-maximum thermometers were used to record temperatures. They were attached to a sufficiently big and dense shade tree about 2 meters above ground near the experimental sites. A wooden roof (30 x 30 cm) additionally protected

the external sensor from rain and sun. At the IITA Station (following referred to as IITA), data from the IITA weather station were used.

Soil humidity. Starting with DAP 0 (DAP = days after planting) right before sowing, soil samples were taken every two weeks up to DAP 70 in the last three successive seasons (I/96: 0-10 cm; seasons II/96, I/97: 0-60 cm). Since the differences in humidity between plots were regarded as comparatively weak in season I/96 at a depth of 10 cm, the depth was increased to 60 cm (0-60 cm) for the following two seasons. Two pairs of samples per plot were assigned to one glass container each and used as mean score per plot. To avoid bias by water loss, all samples were weighed *in situ*. They were brought to the oven (80°C for 120 hours or 100°C for 96 hours) and weighed afterwards. The difference accounted for by water loss was used as a response variable.

Germination. Germination was controlled (except for season I/95) some weeks after sowing (DAP 42) while counting all missing plants within five randomly selected rows per plot out of 12 to 16 in total (depending on region). Scores are means per row. Possible post-sowing differences in plant densities due to rodents, predators, and soilborne pathogens were thereby accounted for. Plant phenology was expected to be influenced by plant density.

Plant density. Since the fields were prepared in the local manner with the assistance of farmers, the ridges, which are a common technique, varied slightly in distance (particularly on-farm). Plots therefore had different numbers of lines, which accounts directly for plant density. Counting all lines per plot, given the number of plants per line, has controlled for this effect.

Statistical analysis. Nutrient levels in the soil were compared on a per plot basis, using mixed models ANOVA. If found necessary, after being checked for normality and homoscedasticity on the standardized residuals (Korie, pers. comm.), data in ppm or meq were $\sqrt{(x + {}^{3}/_{8})}$ transformed (Carsky, pers. comm.), those in percent to arcsine $\sqrt{p}$ (Sachs 1984). During the last two seasons (II/96, I/97), when soil sampling was repeated after harvest, a mixed models ANOVAR (ANOVA for repeated measures) was applied (O'Brien & Kaiser 1985; Littell et al. 1996); the pre-sowing scores and those after harvest represent the two time points.

Precipitation, mean temperature, and mean humidity were compared using mixed models ANOVA, considering data ranging from one week before sowing up to DAP 70. Precipitation, temperature, and humidity were averaged per week. Statistical comparison was carried out between regions and between seasons within regions. A $\sqrt{(x + {}^{3}/_{8})}$ transformation was applied if found necessary. Since no replication was used per season, no statistical comparison was performed on this level.

Soil humidity was measured every two weeks from DAP 0 (time of sowing) until DAP 70, being equally spaced for every season and region. An ANOVAR for mixed models was fitted to allow for profile comparison. The scores, being proportions, were arcsine $\sqrt{p}$ transformed.

Data for missing plants (not germinated) and plant densities were, if necessary, $\sqrt{(x + {}^{3}/_{8})}$ transformed. Since these counts consisted of one single event per season, standard factorial ANOVA for mixed models was used.

After each ANOVAR, least squares means were conducted for separation of means. To account for *a priori* chosen treatment differences, orthogonal contrasts were selected. Since contrasts can represent combinations of comparisons as "weighted sum of means" (Hand & Taylor 1987, p. 10), they were used to compare different clusters, e.g., first growing seasons (I/95, I/96, I/97) against second growing seasons (II/95, II/96), or no mulch (control) versus mulch ([*Senna siamea* (called *Senna*) + *Imperata cylindrica* (called *Imperata*)]/2).

To distinguish seasonal and regional patterns, a factorial ANOVA across time was preferred over repeated measures. Particularly distinct profiles within each season and between first and second rainy seasons did not allow proper comparisons of trends. Instead, seasons and regions were incorporated as additional factors. For comparisons between regions and between seasons within regions, replications were nested within region and season, respectively, to use a hierarchical error term (Korie, pers. comm.). The only exception was soil humidity. The underlying data structure allowed an ANOVAR approach, including regional comparisons.

A *P*-value of 0.05 has generally been used to judge significance. If reckoned important, higher levels of *P*, $0.07 \geq P \geq 0.05$, were considered as marginal responses. They are followed by the expression $P \geq 0.05$ in the text. *F*-values are marked with one star (*) if $0.05 > P \geq 0.01$ and with two stars (**) if $P < 0.01$.

Different methods of addressing parasitism

There are different methods proposed by van Driesche & Bellows (1988) and van Driesche et al. (1991) for addressing the question of total losses from parasitism. The authors' recommended recruitment approach was not followed, however, for several reasons:

1) It was not considered necessary to assess the total parasitism rate per generation since the aim of the study is to compare differences in parasitism rates between treatments rather than measuring an overall potential in the system ("comparative losses" instead of "total losses"). A relatively high precision and reliability of the numbers was accounted for by use of repeated measures not relying on single events only.
2) Secondary mortality effects (e.g., micro-organisms in the field, sluggish defense behavior against predators due to parasitism [van Driesche & Bellows 1988]) not directly ascribed to parasitism were regarded as not varying sufficiently between treatments under these short-term conditions to bias the results.
3) Simmonds (1948) recommended caution when removing samples from the field since those organisms are excluded from further possible attack. The resulting apparent parasitism would be an underestimate of true parasitism. The fluctuations in pest and antagonist populations would render a single sample inadequate. The problem was tackled by taking a series

of samples over time (repeated measures) to attain more realistic estimates. However, since samples were removed from all plots, the problem of underestimation was a general one, not an object of bias among treatments.

4) A total of 48 treatments over three regions far apart did not permit the required monitoring density that would be needed for recruitment techniques (van Driesche & Bellows 1988).
5) Some insects pose certain sampling difficulties for measuring recruitment rates and even densities under field conditions; one of these are borers (van Driesche et al. 1991). Eggs of *M. vitrata* are extremely difficult to find in the field (Taylor 1967). Larvae of all stages are spread over the entire cowpea plant, mainly hiding in flowers, pods, and soil litter without much wandering on the surface. At the end of larval development, late instars leave the plant to pupate in the soil (Taylor 1978). As stated by Wolda (1988), insects in humid tropical regions do not show distinct generations or moments of susceptibility like diapause (van Driesche 1983). There is no generational synchrony ("stable moment" [van Driesche 1983, p. 1618]). Additionally, the input/output rate of parasitoids into the or from the system is highly overlapping, as is often the case in nature. Following the classification of van Driesche (1983), *M. vitrata* and *M. sjostedti* can be regarded as free-living hosts showing neither stable moments nor leaving durable artifacts (e.g., leaf mines) that would allow a representative sampling on a generational basis. Instead, there exists a permanent loss from the system and at no time will all parasitoids and hosts be present to sample. This is especially true for *M. vitrata*, which has many susceptible stages as the target of different parasitoids. These parasitoids belong to a system where oviposition and emergence cover different host stages, which is recognized as the most difficult type to assess generational levels of parasitism (van Driesche 1983).
6) *M. vitrata* (larvae and adults) exhibits a type of nocturnal activity (Taylor 1978; Tamò, pers. comm.; Arodokoun, pers. comm.) that poses difficulties in non-destructive sampling during daytime.

Hence, there is no method available that is readily applicable for hosts that lack suitable periods of stability (van Driesche 1983). Under these circumstances and the underlying hypotheses, the death rate analysis (van Driesche et al. 1991) was reckoned most appropriate. It is relevant where neither densities nor recruitment rates can be measured, but only mortality rates.

Basic points of attention

Certain critical issues were considered throughout the entire trial period in order to render results most comparable.

Sowing dates varied only by a difference of one day between Tokpa/Ayou and Lema and two days between Tokpa/Ayou and IITA as they were sown on three consecutive days of the same week. This was not always easy since the onset of reliable rainfall conditions varied be-

tween the mainly monomodal region Lema and bimodal regions Tokpa/Ayou and IITA. However, this simultaneousness was considered more important while looking at establishment of pest populations, the pressure of which increases with delayed dates (Summerfield et al. 1974; Ezueh 1982), than to sow with the first onset of rains in each region individually. An increased comparability between regions was achieved by putting up with a slightly later sowing date for all three regions together.

For purposes of statistical analysis, spacing of sampling events was always equal. From the first sampling for the first season in 1995, the same day of the week was kept for each region up to the last harvest in August 1997. The same applies to host plants. All possible exercises ever done during the period were carried out on the single day assigned for sampling. The only exception was the exposition of eggs for parasitization studies on *M. vitrata*. Since these activities followed their distinct rhythm (preparation in the greenhouse, exposure to adult moths), they were moved to another day of the week apart from the regular sampling days. This exercise was comparatively time consuming.

The order of different exercises was also the same across regions and time. The order of execution on each sampling day was as follows:

1) Flower sampling in alcohol in cowpea (the order of blocks to be sampled remaining the same throughout the season).
2) Second flower collection (for parasitism studies) in cowpea.
3) Flower sampling in alcohol in host plants.
4) Phenological studies.
5) Soil sampling for humidity.
6) Pod harvesting for studies on parasitism.

Phenological studies on plants were always carried out by the same two experienced persons. Because pre-tests of comparative counting of organs on plants between the two persons to check for bias showed differences in results, the same plots were assigned to each person during the whole season. A systematic error could be excluded since the chosen plots assigned to each person did not consist of the same treatments over blocks. Furthermore, by applying this method, a potential bias within sampling days (between individually assigned plots) was put up with in favor of eliminating error across sampling dates (trends), the latter being considered crucial for profile analysis.

Throughout, the idea was to reduce sampling error and not to artificially increase the naturally occurring, often high variability of ecological data.

Statistical analysis

The underlying data were analyzed with the Statistical Analysis System (SAS – Version 6.12; The SAS® Institute Inc., Cary), GENSTAT (Version 5, Release 3.2; Lawes Agricultural

Trust) and the Statistical Package for the Social Sciences (SPSS – Version 8.0; SPSS Inc., Chicago). The weekly sampling intervals with equal spacing allowed application of repeated measures methods as structured multivariate analysis (Hand & Taylor 1987; Sokal & Rohlf 1995a; Vanleeuwen et al. 1996). This type of analysis permits both between-subjects and within-subject analyses. Whereas the between-subjects component is principally based on ANOVA techniques, the within-subjects analysis tackles variation within the same subject being measured repeatedly over time. The latter forms individual profiles to be studied for differences over time. This approach combines factorial tools (between-subjects) with regression facilities (within-subjects) on the time dimension, and is constructed as a general linear model (Searle 1971; Littell et al. 1996).

Because interest lies in comparing trends rather than responses on individual time points, multivariate and univariate methods (ANOVAR) were used to test divergence in response profiles over time (Kenward 1987; Marascuilo & Serlin 1988; Snedecor & Cochran 1989; Scheiner & Gurevitch 1993; Littell et al. 1996). ANOVAR techniques are reckoned to be appropriate for addressing the profile problem (Greenhouse & Geisser 1959) and are considered more powerful than MANOVAR methods (Potvin et al. 1990), given that some assumptions are met. Mixed models procedures were used to account for separation of mixed and random effects that would fit a more appropriate error term. The factors (NPK, mulch, seasons, regions) were assigned as fixed effects since their levels were clearly defined by the hypotheses and were of exclusive interest. Replications or blocks were defined as random, representing only a small and fragmentary portion out of an infinite entirety (Geisser & Greenhouse 1967; Köhler et al. 1996). When testing repeated measures designs the type I analysis was used as suggested by Littell et al. (1996), providing sequentially formulated hypotheses that are appropriate for polynomial models. In all other purely factorial cases without testing on profiles, the type III analysis was followed introducing all factors at the same time.

Continuous responses. For continuous patterns of insect abundance (counts per unit), phenological measurements on plants, soil humidity, missing plants, yields, temperature, and precipitation, as well as soil nutrient levels, the mixed models procedure (PROC MIXED in SAS) was used. Traditionally, repeated measures designs are analyzed with mixed-model ANOVA (O'Brien & Kaiser 1985). The potential distinction between fixed and random effects furnishes multiple error terms, which are more appropriate for hypothesis testing (Geisser & Greenhouse 1967; Searle 1971; Underwood 1981; Köhler et al. 1996; Littell et al. 1996). A second aim was to control variance and covariance patterns, also known as compound symmetry (Huynh-Feldt condition) and circularity condition (sphericity), two somewhat strict assumptions that typically are not met in biological growth data or, more generally, in repeated measures data (Greenhouse & Geisser 1959; Huynh & Mandeville 1979; O'Brien & Kaiser 1985; Hand & Taylor 1987; Marascuilo & Serlin 1988; Crowder & Hand 1990; Potvin et al. 1990; Everitt & Dunn 1991; Scheiner & Gurevitch 1993; Vanleeuwen et al. 1996; SAS/STAT Software 1997). Having this in mind, the split-plot approach, treating time as a sub-plot, could

not be used (Box 1950; Matthews et al. 1990). This is a crucial point, where errors occur regularly (Gomez & Gomez 1984; Monlezun et al. 1984; Littell et al. 1996; Vanleeuwen et al. 1996). Introductory studies on representative data sets (SPSS repeated measures ANOVA procedure) showed that the recommended operation of adjusting the degrees of freedom by a correction factor ε was not suitable for managing the effect of an unknown covariance matrix. Comparisons using the Box-Geisser-Greenhouse parameter ε (regarded as overly conservative) and the Huynh-Feldt ε (recommended as more liberal) (Greenhouse & Geisser 1959; Huynh & Feldt 1970) proved that this procedure was not adequate to attain exact *F*-distributions. In repeated measures designs the assumption of independence of error components applying to normal ANOVA is generally violated due to effects of time (temporal autocorrelation) or position (spatial autocorrelation), which themselves give rise to a certain correlation (Box 1954; Legendre 1993). In particular, the variance increases (common in growth data) and the correlation decreases simultaneously the farther apart time points lie (Kenward 1987). This is known as autoregressive pattern or isolation-by-distance models (Legendre 1993). Temporal autocorrelation should not be removed before modeling, but rather be accounted for by the covariance structure. Partial effects like comparisons or contrasts or simple effects are even more unstable under disregard of sphericity assumptions (Boik 1981; Mitzel & Games 1981). Nowadays, the problem identified by Box (1954) and O'Brien & Kaiser (1985) of artificially inflating *F*-values of omnibus tests can be overcome by use of the repeated statement (SAS) for the within-subjects factor (Littell et al. 1996). The repeated approach (along with a repeated statement) tackles the phenomenon of correlation between time points, which is called serial correlation by Odulaja et al. (1994), or, in general, mutually dependent response variables ("albeit complex," Scheiner & Gurevitch 1993, p. 96) and variation within experimental units. Thereby, compound symmetric, autoregressive, or unstructured correlation matrixes can be used alternatively (Littell et al. 1996). The mixed models methodology has advanced rapidly and became computationally feasible only in recent years. It is considered necessary for many statistical approaches (Littell et al. 1996).

Each data set was checked for normality and homoscedasticity on the standardized residuals. Mostly, continuous response variables had to be squareroot transformed ($\sqrt{(x + c)}$; c = constant), and percentages generally were arcsine transformed (arcsine $\sqrt{(p + c)}$; c = constant for 0%) (Gomez & Gomez 1984; Sachs 1984) to aid additivity of effects and to stabilize the variances (Perry 1986; Snedecor & Cochran 1989). Thereafter, the covariance matrix, which best handles the underlying correlation structure between time points (Littell et al. 1996), was fit through guidance of Akaike's information criterion and Schwarz's Bayesian criterion (Littell et al. 1996; SAS/STAT Software 1997), being autoregressive or unstructured. This is a crucial point of attention since the resulting fit influences the level of significance (Greenhouse & Geisser 1959; Huynh & Feldt 1970; Huynh & Mandeville 1979).

First, the time variable was treated as qualitative, therefore introduced as factor. Results were controlled for time-by-treatment interactions as well as all the respective main effects.

Because the variable time also can be considered as quantitative, the response variables were modeled as a polynomial function of time in a second approach (Box 1950). Since the time variable has quantitative levels, it is a natural candidate for orthogonal polynomial trend contrasts (O'Brien & Kaiser 1985). Handling time as a regression variable gave smoothed trends of treatments over time (Littell et al. 1996). The individual time-by-treatment interactions were examined by linear and quadratic terms using orthogonal polynomials to fit the curves (Snedecor & Cochran 1989; Zolman 1993; Sokal & Rohlf 1995b). As a third approach, the responses on a daily basis were cumulated, to be investigated on the respective sum with a normal mixed model ANOVA.

The inherent response profiles were investigated following methods of profile analysis. Three hypotheses are checked in descending order of importance: 1) *parallelism hypothesis*: comparison of shapes of response curves, a test of homogeneity of group profiles (interaction of time variable with treatment factor); 2) *levels hypothesis*: comparison of levels of the response curves (treatment main effects); 3) *flatness hypothesis*: determination of slopes of the response curves (time main effect) (Greenhouse & Geisser 1959; Hand & Taylor 1987; Kenward 1987; Scheiner & Gurevitch 1993; Norusis 1994). In a further step, partial effects such as simple effects and contrasts were investigated (O'Brien & Kaiser 1985). Polynomial contrasts were accommodated on the time variable and the time-by-treatment interaction to study progression of pest populations over time. Helmert contrasts as well as repeated contrasts (Hand & Taylor 1987; Norusis 1994) were applied to treatment and time main effects as well as their respective interactions as planned comparisons (*a priori*) (Barker & Barker 1984; Köhler et al. 1996), both being orthogonal (Barker & Barker 1984; Hand & Taylor 1987; Everitt & Dunn 1991), to attain a more detailed insight into patterns of differences (shapes of profiles). These interaction contrasts were constructed using the Kronecker product (or direct product) of two vectors (O'Brien & Kaiser 1985) to obtain the interaction vector. The degrees of polynomials mostly were limited to the second order (quadratic), since the lower order trend contrasts are believed to account for most of the meaningful variation in the data. The higher order ones represent mostly randomness or noise (O'Brien & Kaiser 1985).

Orthogonal contrasts were used instead of multiple comparisons of means (*post hoc*), which are often regarded as not appropriate (Ramsey 1978; Perry 1986; Day & Quinn 1989; Saville 1990; Holzer & Precht 1992; Scheiner & Gurevitch 1993; Thomson, unpublished; Nokoe, pers. comm.) to control the experimentwise (familywise) error rate (Ryan 1960; O'Neill & Wetherill 1971; Russell & Spiegel 1976; Kirk 1982; Jones 1984; Shaffer 1986; Simes 1986; Hand & Taylor 1987). The analyses were conducted applying "protected ANOVA" procedures (Hummel & Sligo 1971; Bock 1975; Barker & Barker 1984; Huberty & Morris 1989; Scheiner & Gurevitch 1993). Only if overall (multivariate) analysis led to rejection of the null hypothesis (H_0), separate univariate analyses could follow. But still, this was done with caution since there is strong evidence that univariate ANOVAs on adjacent time points (multiple univariate tests) are correlated (Matthews et al. 1990). The resulting *F*-tests will not be independent (Saville

1990; Scheiner & Gurevitch 1993). Assuming an underlying autoregressive correlation structure, any univariate ANOVA on one time point is likely to show similar results more often on adjacent time points (Matthews et al. 1990). However, this topic is still regarded as controversial (Huberty & Morris 1989).

Another problem is the artificial division of naturally occurring continuously changing biological variables by use of multiple univariate tests. Significance and non-significance on succeeding time points within the same curve seem not to be a sensible way to divide sets of repeated responses (Matthews et al. 1990). On the other hand, the approach suggested by Matthews et al. (1990) of summarizing the responses to one number (cumulative value, area under a curve) is still not satisfactory for measurements on a time scale. This method avoids correlation problems, but does not furnish conclusions on the profile trend. To overcome the profile problem, among several authors, Sétamou et al. (1995) used so called “borer days”, Tamò (1991) looked at “thrips days”, and “mite days” were investigated by Yaninek et al. (1989, 1990); all three approaches combine abundance levels and duration between sampling events. However, this approach still leaves some information on trend unused while not accounting for autocorrelation. With this in mind, differences in responses were sought by the use of mainly multivariate techniques (ANOVAR). As a means of explaining exceptional underlying patterns in-depth, univariate ANOVAs were carried out where considered necessary.

Categorical responses. Parasitization by antagonists and pod damage by *M. vitrata* are categorical responses. Since these are proportions rather than counts, techniques not assuming normality have to be used. The appropriate access to this kind of data is through application of generalized linear models (GLIM) (Nelder & Wedderburn 1972; Liang & Zeger 1986; Dobson 1990; Diggle et al. 1994; Lipsitz et al. 1994). One of the few procedures that handle data with a binomial distribution and a correlation within-subjects (by use of generalized estimating equations, GEE) at the same time is the GENMOD procedure (SAS), following the underlying general formula:

$$\binom{k}{y} p^y q^{k-y} = \frac{k!}{y!(k-y)!} p^y (1-p)^{k-y}$$

where k = trials, y = successes (events), p = probability one (‘yes’), q = probability two (‘no’) (Sokal & Rohlf 1995a, p. 72).

This technique was preferred over CATMOD (SAS), which is considered unnecessarily complicated for the same type of analysis (Korie, pers. comm.). GENMOD handles data on success and failure (Sokal & Rohlf 1995a) or events per trial (SAS/STAT Software 1997) using raw data instead of percentages or proportions. It therefore takes into account different sample sizes (trials), for which the outcoming successes (events) are weighted. During the procedure, the data generally are logit transformed. Like the mixed models approach, the repeated

measures techniques as well as the particular covariance structure apply for the GENMOD procedure in the same way.

Significance was judged on the $P = 0.05$ level. If necessary and important as results, higher levels up to $P \leq 0.07$ were considered as marginal responses. Principally, results and data were presented following the rules of the Entomological Society of America (ESA) (Entomological Society of America 1992). Means presented in the text are marked with [^{d}] when they were detransformed from analysis; those without the letter were obtained from analysis without transformation or were raw data in some indicated cases. Despite the phenomenon that detransformed data are not identical with the means of the originating raw data, they were used for presentation in all cases where transformations were applied before analysis since results of analysis clearly were attributable to these transformed values (Korie, pers. comm.).

2 Impact of organic mulch combined with two levels of NPK fertilizer on the development and yield formation of cowpea, *Vigna unguiculata* (L.) Walp. (Leguminosae)

ABSTRACT Mulch is a traditional material used by African farmers to preserve soils from physical and nutritional degradation. This chapter centers around the development and yield formation of the cowpea plant, *Vigna unguiculata* (L.) Walp. (Leguminosae), at three different locations in Southern Benin, as influenced by the application of different mulch types in combination with two levels of NPK fertilizer. Data on plant size (number of nodes), reproductive potential (number of flowers), and yield formation (number of pods) were collected periodically. These three levels of the plant were exposed to external influences: soil properties, climate, and attacks by the pod borer and the flower thrips. Different mulch types in combination with NPK fertilizer were applied to modify the soil properties. Weekly counting of nodes, flowers, and pods, as well as the abundance of both pests in flowers allowed the monitoring of these interactions, which were analyzed using multivariate repeated measures. Mulch was found to affect plant growth only marginally. This was ascribed mainly to the short-term conditions linked to the cowpea variety used, which left most of the beneficial mulch effects underexploited by the time the plant was ready to be harvested. Applied chemical fertilizer expectedly showed strong impact on vegetative growth and, to some extent, on flower set. However, the poorer the soils were the more plants were forced into vegetative overgrowth to the detriment of reproductive parts. If coinciding with the early reproductive development of cowpea, thrips exhibited a dominant influence, causing sufficient damage to flowers to result in subsequent loss in pod set. The results of this study indicate that none of the factors under investigation dominated in terms of an overall main effect. They were, rather, found to interact strongly, hardly permitting clear-cut predictions. It is recommended to avoid direct NPK application to cowpea since the results do not justify the high input costs. Furthermore, the effects of mulch need to be appraised under long-term conditions, as they would be more likely to reveal its known beneficial effects. The undoubtedly high yield potential of cowpea, which is noted for its unreliable seed yields, is put at risk the more the sowing date is delayed. As farmers' practices indeed indicate, cowpea production in late seasons is not encouraged where the crop cannot be protected efficiently.

Cowpea is grown under a wide range of climatic and soil conditions, including very dry and agriculturally difficult places (Summerfield et al. 1983; Summerfield & Roberts 1983), and is able to yield under various extreme conditions like drought stress avoidance (Turk & Hall 1980a; Hall & Grantz 1981) and drought resistance (Turk & Hall 1980c; Turk et al. 1980). As a legume it acts in symbiosis with *Rhizobium* to assure nitrogen fixation (Sellshop 1962; Summerfield et al. 1974; Eaglesham et al. 1977) and it also has the ability to compensate for losses on vegetative and reproductive tissue (Wien & Tayo 1979).

Mulch is used widely by African farmers to fight against the effects of drought or to reduce erosion in areas with high precipitation (Slingerland & Masdewel 1996; Müller-Sämann & Kotschi 1997); farmers also largely appreciate the positive effects of mulch on soil and plants (Macmillan 1952; Masefield 1957; Terada 1971; Rachie & Roberts 1974; Kamara 1980; Schoningh 1985; Daisley et al. 1988; Yih & Vandermeer 1988; Gupta & Rao 1989).

In view of the high vegetative productivity of the inner tropics, abundantly growing plant communities offer a cheap source and large quantities of material that could be used for mulch. Were there not serious constraints on the availability of labor during peak field activities and the allocation of considerable amounts of organic matter, as well as traditional antagonisms concerning the use of certain plant materials (e.g., millet straw in Sahelian countries to be used for construction, to feed animals, or to remain on the fields as mulch) (Müller-Sämann & Kotschi 1997), mulch possibly could assist in halting the degradation of tropical soils.

This chapter assesses the influence of organic matter in combination with applied chemical fertilizer only insofar as physiological aspects of the plant are affected. While on the one hand the plants are susceptible to damage by pests, in particular the pod borer and the flower thrips, on the other hand plant physiology can itself influence pest populations. The discussion is by no means an attempt to display fully a complete study on cowpea in an agronomic sense. Rather, the close relationship between plant and pest populations is scrutinized, since this interaction is vital for the comprehension of pests' behavior.

In this context, flowers are the organ of basic interest as both pests strongly rely on them for their feeding and reproduction (Ghesquière 1942; Taylor 1967; Taylor 1969; Taylor 1978; Woolley & Evans 1979; Tayo 1988; Atachi & Ahohuendo 1989; Firempong & Magalit 1990; Tamò et al. 1993b). As attacks to flowers and their subsequent shedding (Taylor 1964; Wien & Tayo 1979; Tamò et al. 1993b; van de Klashorst & Tamò 1995) have various implications for vegetative growth (Lawrie & Wheeler 1974) and thus severely affect economic yield (Rachie & Roberts 1974; Summerfield & Roberts 1983; Summerfield et al. 1983), the plant as a whole needed to be monitored continuously.

A crucial point of attention in this chapter is that the cowpea plant is poised between the influences brought about by mulch and chemical nutrients on the one hand, and its own ability to compensate for pest damage, on the other hand.

Materials and Methods

Counts on plant organs. Phenological evolution was studied once per week at equal time intervals on randomly marked plants. Starting with the young plants two weeks before flowering, on each sampling day the number of nodes, flowers, and pods were counted as they appeared on 10 plants per plot. These plants were excluded from any other exercise to be done in the same fields that would have influenced their generative response, resulting in misleading results on counts. However, these marked plants showed a slightly faster senescence, the big-

ger in size they were and became. Leaves fell off earlier and longer branches were damaged more easily during weekly counting. This effect was most obvious in Lema, where different soils and rainfall patterns often resulted in dense, long-branched plant populations. While counting was suspended at harvest in earlier seasons (flowers were still present), flower counts were continued for three to four weeks after harvest in later seasons in an attempt to reach the point where flower production approached zero. This was not possible when rains continued after harvest because the plants continued to bloom as long it rained. This phenomenon was particularly noticed at the end of the first cropping seasons of each year. The plants were counted by the same two persons throughout the whole trial period.

Flower index. A flower index was developed consisting of the quotient of flower numbers to plant size (nodes); this made it possible to compare reproductive output per vegetative mass. Although plant growth (number of nodes) is a naturally cumulative response, flower production was not cumulated over time since repeated measures were used for analysis. Rather, the actual number of flowers on a given state of growth (number of nodes) along each time point was evaluated. Following the underlying idea of looking at the "fine tuning" over time, it was thought that a cumulated response would leave out information while probably responding poorly to polynomial contrasts.

Statistical analysis. Equally spaced counting dates on phenology allowed application of repeated measures analysis (ANOVAR) (Hand & Taylor 1987; Vanleeuwen et al. 1996). Mean scores of 10 plants per plot were used as responses. ANOVAR for mixed models was carried out, using polynomial trend contrasts for profile analyses. *F*-values were marked with $^{[l]}$, $^{[q]}$, or $^{[c]}$ if tested on the linear (first order polynomial), quadratic (second order polynomial), or cubic trend (third order polynomial), respectively. Data were $\sqrt{(x + {}^{3}/_{8})}$ transformed if necessary.

Flower indexes were created using the quotient of number of flowers and nodes. Before analysis, mean score quotients were arcsine $\sqrt{p}$ transformed, p being the quotient. ANOVAR for mixed models was carried out.

After each ANOVAR, least squares means were conducted for separation of means. Orthogonal contrasts were selected to account for *a priori* chosen treatment differences. Since contrasts can represent combinations of comparisons as "weighted sum of means" (Hand & Taylor 1987, p. 10), they were used to compare different clusters, e.g., first growing seasons (I/95, I/96, I/97) against second growing seasons (II/95, II/96), or no mulch (control) versus mulch ([*Senna siamea* (called *Senna*) + *Imperata cylindrica* (called *Imperata*)]/2).

To distinguish seasonal and regional patterns, a factorial ANOVA across time was preferred over repeated measures. Particularly distinct profiles within each season and between first and second rainy seasons did not allow proper comparisons of trends. Instead, seasons and regions were incorporated as additional factors. For comparisons between regions and between seasons within regions, replications were nested within region and season, respectively, to use a hierarchical error term (Korie, pers. comm.). The only exception was soil humidity. The underlying data structure allowed an ANOVAR approach, including regional comparisons.

A *P*-value of 0.05 was generally used to judge significance, although higher levels were considered as marginal responses if reckoned important. *F*-values were marked with one star (*) if $0.05 > P \geq 0.01$ and with two stars (**) if $P < 0.01$.

The exact description of experimental sites and the research design, auxiliary data like climate and soil properties, and a detailed description of the statistical approach were discussed completely in Chapter 1.

Results

I. Site characteristics as auxiliary data bases

Regional differences

All regions

Soil sampling. Carbon quantities in the soil were highest in Tokpa/Ayou, significantly surpassing IITA and Lema ($F = 55.9^{**}$) (Table 2.1.). Lema was situated at the lower end. The particular contribution for the significant effect between Tokpa/Ayou and Lema occurred in all five seasons, between Tokpa/Ayou and IITA in seasons II/95 and I/96, and between IITA and Lema in seasons II/95, I/96, and II/96 ($F = 2.5^{*}$). The highest cation exchange capacities were measured in Tokpa/Ayou; these were significantly higher than the other regions ($F = 44.4^{**}$). Seasons I/95, II/95, I/96, and I/97 were principally responsible for the variation between Tokpa/Ayou and IITA, while the first four seasons (I/95-II/96) accounted for the difference between Tokpa/Ayou and Lema ($F = 2.6^{*}$). Lema significantly led the three regions in potassium soil content, and IITA yielded significantly lowest values ($F = 11.9^{**}$). Magnesium concentrations were again highest in Tokpa/Ayou against IITA and Lema, the latter being significantly lower than the two other regions ($F = 54.1^{**}$). Exactly the same significant order appeared for nitrogen ($F = 70.7^{**}$). Concerning phosphate, IITA was superior to both Tokpa/Ayou and Lema ($F = 6.1^{**}$). For the difference between IITA and Lema, seasons II/95 and I/97 contributed significantly to the general effect, whereas between IITA and Tokpa/Ayou this was limited to season II/95 ($F = 3.9^{**}$). The highest pH-levels (means across depths and seasons) prevailed in Lema (pH 6.0) compared with Tokpa/Ayou (5.8), and were lowest at IITA with a pH of 5.2 ($F = 74.3^{**}$). This main effect was based principally on the significant variation between Lema and IITA for seasons I/95, II/95, I/96, and I/97, the one between Lema and Tokpa/Ayou on seasons I/96 and I/97; the lower value for IITA was sig-

nificant during seasons I/95, II/95, and I/97 ($F = 8.4^{**}$). To summarize, Tokpa/Ayou revealed superior values for carbon, cation exchange capacity (CEC), magnesium, and nitrogen. Lema showed best results for potassium and pH, and the lowest levels of carbon, magnesium, and nitrogen. IITA had the most favorable phosphate levels but the lowest pH values. All measurements appeared in higher concentrations or at higher levels in the upper soil stratum (0-10 cm) compared with the lower layer across all regions.

Precipitation. All regions received about the same amount of rainfall from one week before sowing until DAP 70 across all five seasons. A slight tendency is visible in the raw data favoring IITA (402.5 mm) over Lema (389.1) and Tokpa/Ayou (352.3) in mean rainfall over the five seasons (see Tables 2.2., 2.4., 2.6.). Raw data were used for presentation since the analysis displays means only, which complicates ready application. These differences were not significant, however; rather, there was a significant seasonal main effect across regions. The set of first rainy seasons (I/95, I/96, I/97) obtained roughly the same amount of rainfall among one another (season I/95 being slightly less) as was the case for the two second rainy seasons (II/95, II/96). The two clusters – I/95, I/96, I/97 versus II/95, II/96 – were significantly distinct from each other ($F = 34.5^{**}$) but not within the clusters.

Temperature. Lema was the warmest region of the three (Tables 2.3., 2.5., 2.7.). With a mean temperature of 26.4°C it was significantly warmer than IITA and Tokpa/Ayou; the latter was the coolest region with a mean temperature of 26.0°C ($F = 5.2^{**}$). IITA was only slightly warmer than Tokpa/Ayou. Additionally, seasons differed significantly from each other across regions. II/95 (26.8) reached highest temperatures and was significantly hotter than season I/95 (26.3), II/96 (26.1) and I/97 (25.5) ($F = 11.6^{**}$). Season I/97 remained the coolest. Seasons I/95, I/96, and II/96 did not differ significantly in temperature.

Soil humidity. None of the main effects (mean across time) resulted in a real difference, either by region or by season. The same obtained for the profiles (trends) by region over time (DAP) and by season over time. These lower order interactions were invalidated by the higher order interaction including region, season, and time (DAP). Averaging across time (DAP), no absolute differences (levels hypothesis, Scheiner & Gurevitch 1993, p. 120) existed between regions, due to crossover of regional profiles (Fig. 2.1.). An investigation of the profiles in terms of the trends shows that IITA differed from Lema in season I/96 versus II/96 on a linear trend ($F = 25.7^{**}$). The profiles in general were lower for Lema than for IITA during I/96 and II/96. During I/97 the curve for Lema was moving closely with IITA, both indicating a modest low between DAP 42 and DAP 56. An early peak at IITA during I/96 was followed by a slight decrease towards the end of the season. Lema peaked two weeks later at DAP 28 from a very low level and then returned to the low level. Soil humidity continued rising to the onset of flowering (DAP 42). Lema and IITA showed a common peak at DAP 42, right to the onset of flowering in Lema and one week before its start at IITA. No profile differences between IITA and Tokpa/Ayou were uncovered for I/96 and I/97. Trends for I/96 versus II/96 and II/96 versus I/97 were distinct from each other on the second order polynomial. During I/96 and I/97

the humidity profile at IITA crossed the one for Tokpa/Ayou very early (DAP 14 [I/96] and DAPs 14, 28 [I/97]); this was the opposite of the situation in II/96, where a slight crossover occurred at DAP 42 before the onset of flowering at IITA. Apart from that, IITA's profile was lower than that of Tokpa/Ayou. Lema and Tokpa/Ayou were different in profiles in all three seasons (quadratic trend). While the profile for Tokpa/Ayou remained stable through time during I/96 and smoothly rose to a climax at DAP 56 in II/96, the curves for Lema fluctuated considerably with distinct lows and peaks. As for I/97 the shape of both curves did not diverge particularly, marking out a single overlap at DAP 14. Apart from this overlap, the response for Lema remained at a lower level compared with Tokpa/Ayou.

Germination. A region by season interaction revealed differences on II/95 and II/96 ($F = 14.1^{**}$). During II/95, IITA (8.7^{d} missing plants per row) suffered higher losses (not germinated seeds) than Lema (1.0^{d}); in the same way Tokpa/Ayou (8.4^{d}) recorded more losses than Lema. In II/96, having sustained significantly the highest losses, IITA (15.6^{d}) showed lower germination than Lema (3.7^{d}), while losses were highest in Tokpa/Ayou (19.1^{d}).

Plant density. The use of a tape measure during sowing at IITA led to the highest row numbers per plots resulting in highest plant densities. Plant numbers of $53{,}846^{d}$ plants per hectare were significantly higher than in both on-farm regions: Lema with $42{,}970^{d}$ plants and Tokpa/Ayou with $40{,}653^{d}$ plants ($F = 933.1^{**}$). (A number to the power of d [^{d}] indicates that this is a detransformed value from analysis.) The densities in the two on-farm regions Lema and Tokpa/Ayou were significantly different as well.

On-farm regions

Soil humidity. There was a slight, non-significant NPK main effect across regions (Tokpa/Ayou, Lema) and seasons in favor of treatments, where no NPK fertilizer was applied (NPK^{-}). These treatments were tendentiously more humid ($P \geq 0.05$) although not significantly so. Note that in the following text NPK^{-} is used for plots where no fertilizer was applied and NPK^{+} represents those that received NPK fertilizer.

Germination. A distinct NPK effect predominated for both regions and across seasons ($F = 35.0^{**}$). NPK^{-} resulted in significantly lower germination (3.8^{d} missing plants per row) than did NPK^{+} (2.8^{d}).

Seasonal differences within the same region

Tokpa/Ayou

Soil sampling. Carbon contents of both soil layers were equal. The cation exchange capacity in the upper stratum was higher in season I/95 compared with the following seasons ($F = 26.7^{**}$). In the lower layer season II/96 was less than I/95. As for potassium, values in season I/95 were better than in all other seasons for the superficial stratum ($F = 2.9^{*}$). Season II/95 was also higher than seasons II/96 and I/97. In the lower layer season II/96 had lower concentrations than seasons II/95 and I/96, and season I/97 was also lower than I/96. For both strata together season II/95 was superior to II/96. Magnesium was found for seasons II/95 and I/96 to exceed seasons I/96 and I/97 at depths up to 10 cm ($F = 7.1^{**}$). Season I/97 revealed better results than II/96 at both depths. Nitrogen amounts were higher in seasons II/95 and I/97 than in I/96 and II/96, and season I/95 was superior to II/96 in the upper soil ($F = 5.3^{**}$). For the lower layer season I/97 surpassed seasons I/95, I/96, and II/96. Season II/95 also recorded more nitrogen than seasons I/95 and II/96. Over both depths season I/97 was better than I/96 and II/96, the latter being lower than II/95. Phosphate values were higher for season I/95 than for the remaining ones, and season II/95 exceeded I/97 ($F = 13.0^{**}$). At both depths season I/95 was better than I/96 and II/96. The upper layer was more acid for season II/96 in comparison with season I/95 ($F = 6.0^{**}$); and season II/95 was less acid than seasons I/95, I/96, and II/96. Across both depths, the pH value for season I/97 was inferior to all other seasons. Nutrient concentrations as well as the pH value were always higher in the upper soil strata.

Precipitation. Seasons I/95, II/95, and II/96 received about the same amount of rainfall. Season I/96, thought not differing significantly from I/95, was wetter than II/95 and II/96 ($F = 3.6^{*}$) (Table 2.2.). More rainfall was recorded during season I/97 than for seasons I/95, II/95, and II/96.

Temperature. II/95 was recorded as the hottest (27°C) among all seasons ($F = 11.4^{**}$) (Table 2.3.). The lowest temperatures were measured during I/97 (25°C). Seasons I/95, I/96, and II/96 did not diverge from each other.

Soil humidity. Two effects dominated the results on a seasonal basis. A three-way interaction incorporating the factors season, NPK, and mulch gave evidence of generally lower humidity in II/96 in contrast to I/96 and I/97. However, some of the mulch treatments were equal among seasons on the different NPK levels. No attempt was made to fully formulate all the differences since seasonal differences were of primary interest. A much better impression was conveyed by the comparison of responses among seasons over time (Fig. 2.2a.). I/96 and I/97, being separated by marginal differences, both deviated strikingly from II/96 on the quadratic trend ($F = 26.9^{[q]\,**}$). Humidity started low for I/96, overlapped the profile for I/97 on DAP 14 and DAP 28, and decreased below the level of I/97. Soils in I/96 and I/97 were more humid at

sowing than in II/96. While humidity in II/96 reached its climax at DAP 56, the other two seasons fell to a low. Towards DAP 70 humidity increased markedly for I/96 and I/97 in contrast to II/96, which fell back to a low level.

Germination. I/96 and I/97 had equal germination rates, and at very high levels. II/96 suffered the highest losses (19.1 plants per row), followed by II/95 ($F = 36.7^{**}$). In general, seeds in NPK^+ germinated better ($F = 20.1^{**}$).

Plant density. There was no evidence of differences in plant density according to seasons.

Lema

Soil sampling. On a seasonal comparison carbon contents for the whole soil profile favored seasons I/95 and I/97 over all other seasons ($F = 12.6^{**}$). Seasons I/95 and I/97 had a higher cation exchange capacity than I/96 and II/96, and the capacity was higher for season I/97 than for II/95 ($F = 5.5^{*}$). This effect occurred in both strata. Potassium levels did not vary among seasons. Season I/97 was richer in magnesium than seasons II/95, I/96, and II/96 ($F = 3.8^{*}$). Nitrogen in the superficial layer was found in higher concentrations for season I/95 than II/95 ($F = 4.0^{**}$). Soils in season I/97 contained more nitrogen than in I/95 for the lower soil. For both depths together seasons I/95 and I/97 revealed better contents than seasons I/96 and II/96, and season I/97 additionally scored better than II/95. Phosphate was found to vary in the upper stratum only and it was season I/96 that showed a higher accumulation than the other seasons ($F = 5.8^{**}$). Season I/96 was less acid than seasons II/95 and II/96; season I/97 also had a higher pH level than II/96 in the upper soil ($F = 6.2^{**}$). As for the deeper layer, seasons I/95, I/96, and I/97 were more acid than I/96. Both strata together had in common a higher soil acidity for season II/96 in contrast to I/96. A comparison of the two strata showed that the superficial layer always had higher values and concentrations.

Precipitation. The total amount of rainfall during seasons I/95, I/96 and I/97 was higher than it was for II/96 ($F = 2.8^{*}$) (Table 2.4.). The first growing seasons together (I/95, I/96, I/97) were wetter than the second rainy seasons.

Temperature. Factorial ANOVA did not uncover any seasonal differences (Table 2.5.). However, the use of contrasts suggested that I/96 was slightly warmer (26.9°C) than II/96 (26.1), and marginally superior to I/97 (26.2) ($F = 4.5^{*}$).

Soil humidity. Across seasons and time (DAP) soil humidity was generally higher in NPK^- ($F = 8.1^{**}$). When considering the trend between NPK^+ and NPK^- (Fig. 2.3a.) the profiles separate at DAP 28 in favor of NPK^- ($F = 3.0^{*}$). NPK^- remained relatively stable whereas NPK^+ decreased until DAP 56 then rose and joined the profile for NPK^- at DAP 70. This difference fitted best on the third order polynomial. A comparison of seasons revealed no overall seasonal difference. The trends show that I/96 and I/97 behaved similarly, with the profile for I/96 moving on a lower level comparing the two seasons ($F = 84.1^{**}$). An isolated low for I/96

at DAP 14 remained the only remarkable distinction in profiles for I/96 and I/97. Soil humidity decreased in both seasons to a low at DAP 42 and increased towards the end of the seasons. The profiles differed on a linear trend. II/96 developed contrarily; like season I/96, it had its low at DAP 14. Season II/96 peaked at DAP 42, which was the onset of flowering for all three seasons. This was different from I/96 and I/97.

Germination. II/96 suffered the highest post-sowing losses (3.7^{d} plants per row) ($F = 3.9^{**}$). II/95 (1.1^{d}) did not reveal differences from I/96 (0.6^{d}) and I/97 (1.3^{d}), but I/97 showed higher germination than I/96. However, this latter difference was attached to certain mulch treatments only. There was a clear NPK effect in favor of NPK^{+} (1.9^{d}), where germination was about three times higher ($F = 17.8^{**}$).

Plant density. Because of the high uniformity of data for II/95, I/96, and II/96 the iteration for the estimators did not converge properly. Analysis therefore did not offer useful results out of ANOVA. However, the generated least squares means suggested higher densities for season I/95 (49,600 plants per hectare) and I/97 (48,000) together, compared with II/95, I/96, and II/96, which were uniform (42,666).

IITA

Soil sampling. Carbon quantities as well as concentrations of potassium and magnesium did not vary among seasons. Upper soil cation exchange capacity was more favorable for seasons I/95 and II/96 than for seasons II/95 and I/96 ($F = 6.0^{**}$). For the lower layer, seasons I/95 and II/95 had less capacity than seasons II/96 and I/97, and season I/96 also scored less than II/96. Across depths season II/96 revealed higher capacities than seasons II/95 and I/96. Superficial soil layers were richer in nitrogen for season I/97 than seasons I/96 and II/96 ($F = 3.0^{*}$). In the lower soils season I/95 kept less nitrogen than was the case in seasons II/95 and I/97; I/97 was also richer than II/95 and I/96. Across strata, I/97 recorded better values than I/96. Phosphate reached more elevated levels for season II/95 than in all other seasons ($F = 5.6^{*}$); this effect occurred across depths. Soils were more acid across layers in seasons I/97 and I/95 compared with II/95, I/96, and II/96 ($F = 33.2^{**}$).

Precipitation. The first growing seasons (I/95, I/96, I/97) together recorded higher rainfall than the second growing seasons (II/95, II/96) together ($F = 16.4^{**}$) (Table 2.6.). The respective clusters did not suggest any divergence within each other.

Temperature. Season I/97 (25.5°C) was cooler than I/95 (26.2), II/95 (26.8), and II/96 (26.2) ($F = 4.2^{**}$) (Table 2.7.). II/95 was warmer than I/96 (26.0).

Soil humidity. There was no overall seasonal difference. An investigation of the trends showed that I/96 and I/97 behaved similarly, but with the profile for I/96 moving at a lower level ($F = 61.4^{[q]**}$) (Fig. 2.4a.). Both decreased to a low at DAP 56 (one week after flower onset for the two seasons) and increased towards the end of the seasons. This was significant on the quadratic trend. II/96 showed an opposite trend; having its low at DAP 28, it peaked at

DAP 42, one week before the onset of flowering for the season. It was different from I/96 and I/97, respectively, on a linear trend.

Germination. Plant densities due to poor germination were lowest in II/96 (16.2^{d} missing plants per row), followed in descending order by II/95 (9.3^{d}), I/97 (2.3^{d}), and I/96 (0.7^{d}). The last resulted in highest germination ($F = 143.2^{**}$).

Plant density. Factorial ANOVA did not display differences. However, the use of contrasts showed that season I/95 had lower plant numbers ($52{,}800^{d}$ plants per hectare) than all the other seasons, which were uniform in number ($53{,}993^{d}$) ($F = 7.4^{*}$).

Differences within seasons

Tokpa/Ayou

First season (I/95)

Soil sampling. For all nutrients (carbon, potassium, magnesium, nitrogen, phosphate) and pH, higher concentrations were observed in the layer from 0 to 10 cm depth (Table 2.1.). For carbon, potassium, and magnesium together a difference between plots (across both depths) was observed. The plots to which the control was assigned later, showed lower concentrations of carbon in the control against mulch of *Senna* and against the mean of both mulch types ($F = 3.9^{*}$). The same applied for potassium in the layer of 0-10 cm ($F = 3.7^{*}$). Magnesium was found to be higher in both later mulch treatments ($F = 4.5^{*}$).

Precipitation and temperature. Data for precipitation and mean temperatures are displayed in Tables 2.3. and 2.4.

Plant density. All plots were planted in almost the same densities.

Second season (II/95)

Soil sampling. Carbon, potassium, magnesium, nitrogen, phosphate and pH showed higher scores in the upper soil (0-10 cm) only.

Germination. Germination was influenced by both NPK and mulch. Overall losses in NPK^{-} (9.7 plants per row) were higher than in NPK^{+} (7.9) ($F = 12.7^{**}$). There was also an interaction between the application of NPK and the type of mulch applied. Within NPK^{-} the control had higher losses than *Imperata*, and germination was better with *Imperata* than with *Senna* ($F = 5.8^{*}$). *Imperata* without NPK generally had fewer losses than the control, *Senna*, and *Imperata* with NPK applied. Within NPK^{+}, mulch did not have an impact on germination.

Plant density. As for season I/95, a more or less equal spacing resulted in similar plant numbers per plot.

Third season (I/96)

Soil sampling. Carbon, magnesium, nitrogen, and pH differed in depth only, the values for the deeper layer being lower. Cation exchange capacity revealed a three-way interaction suggesting differences between certain plots only ($F = 4.1^{*}$). There was an inverse relationship of phosphate between some plots. Treatments later applied to these plots showed the following pairs: control without NPK = *Senna* without NPK versus control with NPK > *Senna* with NPK and control without NPK < *Imperata* without NPK versus control with NPK > *Imperata* with NPK ($F = 4.8^{*}$).

Soil humidity. NPK^{+} showed slightly higher humidity levels (across time) ($F = 7.7^{**}$). A marginal deviation between mulch treatments resulted from ANOVA ($P \geq 0.05$). However, use of contrasts pointed to the control, which was found to be significantly less humid than soils covered by *Imperata*.

Germination. Germination in general was very high without visible impact of treatments.

Plant density. Uniform spacing of ridges led to a homogeneous plant density in all plots.

Fourth season (II/96)

Soil sampling. Since soil samples were probed before sowing (called before) and after harvest (called after), a change in nutritional pattern was assessed. Carbon content of the upper soil layer was higher than in the lower level. After harvest carbon increased slightly in both depths (before: 0.8^{d}%, after: 1.0^{d}%) ($F = 112.7^{**}$). In the layer of 0-10 cm, the carbon content increased during the season in the control only ($F = 3.9^{*}$). The time effect for carbon across treatments (before versus after) was observed in both layers. For cation exchange capacity, an inverse time effect was observed between the two depths. The exchange capacity increased on the soil surface (0-10 cm) while it declined in the deeper layer ($F = 35.5^{**}$). Potassium did not change over time but had generally higher contents in the surface layer. The control without NPK had lower potassium contents than the control with NPK where in turn *Senna* without fertilizer was higher than *Senna* with NPK ($F = 3.6^{*}$). Magnesium concentration was higher in the upper layer than in the lower at the start of the season, but increased in both layers be the end of the season ($F = 22.0^{**}$).

Nitrogen was always found in higher quantities in the upper layer. Between the plots for the control and *Senna* an inverse relationship developed during the season in the lower stratum, indicating that the control lost nitrogen whereas *Senna* led to a slight increase ($F = 3.9^{*}$). Phosphate concentrations were higher towards the soil surface. The plots that were fertilized later showed a slightly higher concentration before sowing and treatment application ($F = 17.2^{**}$). Phosphate levels increased more strongly in NPK^{+}, but an increase without help of NPK occurred as well ($F = 6.7^{*}$). Soils were generally more acid downwards (0-10 cm: pH 6.1; 10-60 cm: pH 5.5) ($F = 49.3^{**}$). A significant change occurred over time for the two

depths together ($F = 16.6^{**}$). Close to the surface, the increase was of no importance but in the deeper stratum, the improvement was more obvious.

Soil humidity. Profiles did not differ according to main effects, but mulch showed different humidity conditions due to use of NPK. *Senna* without NPK conserved more humidity in the soil than the control without fertilizer and all treatments under NPK^+, namely the control, *Senna*, and – marginally – *Imperata* ($F = 3.3^{*}$). Humidity in general (time main effect) increased for DAPs 42 and 56, having its peak at the latter event ($F = 41.2^{[c]**}$).

Germination. The comparatively low germination during this season could be improved in NPK^+ (17.8 missing plants per row) from 20 in NPK^-.

Plant density. All plots had the same number of ridges, which extrapolated to 40,000 plants per hectare.

Fifth season (I/97)

Soil sampling. Carbon, cation exchange capacity, potassium, magnesium, nitrogen, and phosphate, as well as pH, did not vary among seasons. Generally, their values were higher on the soil surface.

Soil humidity. Treatments did not exert influence on soil humidity. Humidity rather changed over time ($F = 5.7^{[q]**}$) across treatments (Fig. 2.9a.). Starting high at DAP 0 humidity fell into a low at DAP 14 and increased gradually but not significantly, then declined from DAP 42 to DAP 56, and rose significantly until DAP 70.

Germination. Between NPK^+ and NPK^-, a marginal but not significant difference was observed favoring non-fertilized plots. However, losses were very low: 1.8 plants per row for NPK^- and 1.0 plants in NPK^+.

Plant density. Uniform numbers of ridges achieved plant densities of 40,000 plants per hectare throughout the plots.

Lema

First season (I/95)

Soil sampling. Carbon, potassium, magnesium, nitrogen, phosphate and pH differed between the two strata of soil, having higher values in the upper layer.

Precipitation and temperature. Data for precipitation and mean temperatures are displayed in Tables 2.5. and 2.6.

Plant density. Complete uniformity between plots resulted in 49,600 plants per hectare.

Second season (II/95)

Soil sampling. Carbon, potassium, nitrogen, and phosphate were found in higher concentrations in the upper soil stratum (0-10 cm).

Germination. Use of NPK increased germination by about 1.3%, resulting in almost 99% ($F = 13.4^{**}$).

Plant density. Complete uniformity in the number of ridges per plot resulted in 42,666 plants per hectare.

Third season (I/96)

Soil sampling. The upper stratum of soil had higher concentrations for carbon, potassium, nitrogen and phosphate.

Soil humidity. A slight non-significant difference in levels, in favor of NPK^-, was found after ANOVA (Fig. 2.12a.). However, through investigation of contrasts, a real difference was uncovered ($F = 6.7^{[q]*}$). In the middle of the season at DAP 28 and DAP 42, NPK^- scored marginally higher and lost more humidity until the end at DAP 70. However, this difference in trend was not significant.

Germination. Germination was very high, over 98% (1.0 missing plants per row), and reached over 99% in NPK^+ (0.3 missing plants) ($F = 24.8^{**}$).

Plant density. Uniform plant numbers of 42,666 per hectare were achieved in every plot.

Fourth season (II/96)

Soil sampling. Concentrations for carbon were higher in the upper stratum of soil. During the season carbon increased slightly in the lower stratum ($F = 21.4^{**}$). Cation exchange capacity increased during the season in both depths ($F = 10.3^{**}$). Nitrogen accumulated more in the upper soil. Plots to which *Senna* was applied later, revealed higher nitrogen concentrations before sowing ($F = 4.6^{*}$). Values for phosphate scored higher in the upper soil. Concentrations were found to be higher where NPK^+ had been the treatment afterwards ($F = 28.5^{**}$). At both depths nitrogen was slightly increased during the cultivation period ($F = 37.2^{**}$), but this increase was less than 0.1%. The cultivation process in general increased the pH values in both strata from 5.8 to 6.1 ($F = 14.9^{**}$).

Soil humidity. Treatments did not have an impact on soil humidity conditions. In general, humidity was high at sowing and declined to a low at DAP 14 (Fig. 2.13a.), being significant in trend over time ($F = 87.4^{[c]**}$). Thereafter conditions improved up to a peak at DAP 42 followed by a sharp decline to a low level that remained until the end of cultivation.

Germination. Variation among mulch types indicated that germination under *Imperata* reached about 90% (6.3 missing plants per row) and was inferior to that of *Senna* and the control, the latter germinating most favorably (96%) ($F = 6.3^{*}$).

Plant density. Some 42,666 plants per hectare were attained in all plots due to uniform spacing of ridges.

Fifth season (I/97)

Soil sampling. Carbon, cation exchange capacity, potassium, magnesium, nitrogen, and phosphate, as well as pH, did not differ between seasons. Their values were always higher in the upper stratum.

Soil humidity. Humidity conditions in the soil were different on the NPK effect where soils in NPK^- retained more humidity across time ($F = 6.3^*$). Trends were parallel, showing a lower level for NPK^+ (Fig. 2.14a.).

Germination. Germination was relatively high, at over 96% (2.0 missing plants per row) for NPK^- and close to 99% for NPK^+ (0.7 missing plants). This difference was significant ($F = 9.7^*$).

Plant density. As with all other seasons uniformity of ridge numbers in all plots resulted in overall equal numbers, in this season 48,000 plants per hectare.

IITA

First season (I/95)

Soil sampling. Carbon, cation exchange capacity, potassium, magnesium, nitrogen, phosphate, and pH were recorded in higher concentrations in the upper soil stratum.

Plant density. The use of a tape measure during planting led to uniform row distances, resulting in 52,800 plants per hectare in all plots.

Second season (II/95)

Soil sampling. Concentrations for carbon, cation exchange capacity, magnesium, nitrogen, and phosphate were more favorable in the upper soil layer.

Germination. Germination ranged from 89% to about 94% within mulch treatments without indication for differences.

Plant density. Plant numbers ranged from 53,333 to 55,999 plants per hectare between plots. This was not a significant difference.

Third season (I/96)

Soil sampling. All plots to which the control was later assigned reported a higher concentration of carbon in the upper stratum ($F = 16.5^{**}$). The same pattern on mulch was found

for cation exchange capacity ($F = 3.6^{*}$). Cation exchange capacity, magnesium, nitrogen, and phosphate were generally found to be higher in the surface stratum.

Soil humidity. The control turned out to be more humid (across time) than *Senna, Imperata,* and neem, as well as mulch in general ($F = 3.8^{*}$).

Germination. Germination was very high, over 98%, without showing differences in mulch types.

Plant density. A range of 53,333 to 55,999 plants per hectare did not yield significant differences among treatments.

Fourth season (II/96)

Soil sampling. Carbon was more concentrated in the superficial soil layer. Concentrations of potassium were higher in the upper stratum and increased with the cultivation in this particular layer only ($F = 8.1^{**}$). Nitrogen was found to be higher in the superficial layer. Phosphate followed the same pattern. Plots later assigned *Imperata* had lower concentrations of phosphate than those later assigned *Senna* and neem ($F = 3.8^{*}$). Both depths responded positively to cultivation effects ($F = 14.4^{**}$).

Soil humidity. An impact of mulch on soil humidity conditions was not recorded.

Germination. Germination ranged from about 82% to 86% but did not vary according to mulch types.

Plant density. There were between 53,333 and 55,999 plants per hectare in all plots. This did not yield distinctly different results.

Fifth season (I/97)

Soil sampling. Carbon, cation exchange capacity, potassium, magnesium, nitrogen, and phosphate, as well as pH, did not differ between seasons. Their values were always higher in the upper stratum except for pH, which was similar for both layers.

Soil humidity. Soil humidity was not influenced by mulch.

Germination. Germination responded marginally to different mulch types after ANOVA; the mean separation indicated that the control had germinated better (1.7 missing plants per row) than *Senna* (4.4), which had the highest losses in general. This was about 97% for the control and 93% for *Senna*. The differences were not significant.

Plant density. Some 53,333 and 55,999 plants per hectare were extrapolated for the different plots without indication of significance of variation.

II. Phenological measurements assessing plant development

Regional differences

NPK was not used at IITA. Hence, regional differences were tested in two steps. An overall comparison of the three regions did not consider NPK, leaving mulch as the single treatment factor. The neem treatment (leaves of *Azadirachta indica*) at IITA was excluded as well, which was a special component for the on-station trials only. A second step compared the two on-farm regions Tokpa/Ayou and Lema, controlling for NPK.

All regions

Nodes. Plant sizes were not distinctly different between the three regions across seasons. Among seasons, II/96 produced significantly the smallest plants (20.7^{d} nodes per plant) across regions ($F = 40.0^{**}$) (Table 2.8.). I/95 in turn had higher counts (43.7^{d}) than II/95 (37.8^{d}), I/96 (29.6^{d}), and II/96. II/95 was significantly better developed than I/96 and II/96. Season I/97 (44.9^{d}) did not significantly deviate from seasons I/95 and II/95. There were also seasonal patterns, interacting with region that determined plant growth. During I/95 and I/96 all plants were about the same size across regions ($F = 3.4^{**}$). II/95 revealed a marginal effect where plants at IITA grew in the mean slightly bigger with 42.1^{d} nodes per plant than those at Tokpa/Ayou with an average of 34.1^{d}. However, this variation was not significant. In II/96, plants in Lema were significantly more developed (24.2^{d}) than those at IITA (16^{d}). In I/97, plants remained significantly smaller at IITA (34.3^{d}) compared with Lema (45^{d}) and particularly with Tokpa/Ayou, which had the biggest plants with 56.5^{d} nodes per plant.

Flowers. As with plant size, no distinction in flower production was detected among regions (across seasons). However, seasonal differences came up across regions (Table 2.9.). Plants produced significantly higher numbers of flowers in I/96 (0.78^{d} flowers per plant), with all the other seasons remaining on a lower level ($F = 8.8^{**}$). The flower index was also higher in I/96 compared with the remaining seasons. I/97 also differed from II/96, which resulted in the lowest flower counts and flower index. Furthermore, region interacted with season. II/95 and I/96 did not show significantly different numbers of flowers for all regions ($F = 2.3^{*}$). During I/95, more flowers were set at IITA (0.7^{d}) than at Lema (0.5^{d}). Lema also yielded fewer flowers than Tokpa/Ayou (0.8^{d}). II/96 revealed marginal tendencies only. Flower production at IITA was lowest, lagging behind Lema and Tokpa/Ayou, the two of which were close together. However, these effects were not significant. As for the flower index, Lema yielded the most favorable index in the same season, which was significantly more than at Tokpa/Ayou and at IITA. The latter resulted in the lowest index. I/97 showed a superior flower develop-

ment at Tokpa/Ayou (0.8^{d}) compared with Lema (0.7^{d}) and IITA (0.6^{d}). The numbers of flowers produced at IITA and Lema were roughly the same.

Pods. No differences in pod production were observed between regions (across seasons) (Table 2.10.). In season I/97 (5.9^{d}) significantly highest pod numbers were counted across regions except for Lema ($F = 26.7^{**}$). Whereas the yield for season I/97 was indeed higher than for seasons I/95 (4.2^{d}) and II/95 (1.4^{d}) across all three regions, season I/97 had more pods than II/96 (1.6^{d}) for Tokpa/Ayou and IITA. The inverse was true for Lema, which set more pods in season II/96 compared with I/97. Across all regions pod production in season I/96 was superior to that of seasons II/95 and II/96. At both Tokpa/Ayou and IITA, season I/95 had more pods than seasons II/95 and II/96, but the inverse happened for Lema. Regional differences within season I/95 indicated that plants in Lema formed significantly fewer pods per plant (0.9^{d}) compared with IITA (5.7^{d}) and Tokpa/Ayou, which produced an average of 7.6^{d} ($F = 9.7^{**}$). As for I/96, in the Tokpa/Ayou region significantly more pods were counted (6.2^{d}) compared with Lema with 3.5^{d} pods on average. The latter was marginally but not significantly lower than at IITA with 4^{d} pods. On a lower overall level during II/96 Lema counted significantly higher (2.5^{d}) than IITA with 1^{d} pod only. Pod numbers in Tokpa/Ayou were in between. Generally, highest pod numbers were obtained in I/97. Lema produced significantly lowest with 2.1^{d} pods in contrast to IITA with 7.9^{d} pods and Tokpa/Ayou, leading with 9.1^{d} pods.

On-farm regions

Nodes. In general, plants developed significantly more vegetative substance (number of nodes) across both regions and seasons for NPK^{+} (47.0 nodes per plant) ($F = 109.5^{**}$). On average, plants in NPK^{+} were over 40% bigger than in NPK^{-}. Looking at the simple effects for NPK^{-}, cowpea grew bigger in Tokpa/Ayou compared with Lema ($F = 21.4^{**}$). For NPK^{+}, plants in Lema were barely taller.

Flowers and pods. Counts on flowers and pods did not uncover any effect brought about by use of fertilizer, as far as differences across regions and seasons were concerned. The flower index for non-fertilized treatments (across regions and seasons) was higher, indicating that those plots produced a significantly higher generative than vegetative response. They generated more flowers per nodes in contrast to treatments with applied fertilizer ($F = 11.2^{**}$).

Seasonal differences within the same region

Tokpa/Ayou

Nodes. Plants grew significantly biggest in I/97 with 56.5^{d} nodes per plant, followed by I/95 (43.9^{d}), which showed superior development to II/95 (34.1^{d}), I/96 (31.7^{d}), and II/96

(22.3^{d}) ($F = 15.2^{**}$). Plants were smallest in II/96. II/95 and I/96 did not differ in plant size. Under NPK^{+} plants developed better (40.9^{d}) than did those in NPK^{-} (32.9^{d}) ($F = 13.5^{**}$).

Flowers. All first rainy seasons (I/95, I/96, I/97) were not different in flower production across time, as were all second rainy seasons (II/95, II/96) ($F = 3.5^{*}$). The cluster consisting of I/95, I/96, and I/97 showed on average more flowers (1.0^{d} flowers per plant) than II/95 and II/96 together (0.6^{d}). The patterns for the flower index were the same as for flowers, with the early cluster showing a more favorable index than the late. When seasons were assessed separately, the flower index turned out to be most favorable for I/96 ($F = 14.6^{**}$). I/95 indexed equally to II/95 and I/97, and II/95 was close to II/96.

Pods. Similar to patterns observed for flowers was the yield in pods produced per plant (across time). I/95 (7.6^{d}) did not differ from I/96 (6.2^{d}) and I/97 (9.1^{d}), but I/97 resulted in slightly more pods than I/96 ($F = 24.0^{**}$). Straightforward from flower development the same pattern of seasonal clustering applied for pods. I/95, I/96, and I/97 together (7.6^{d} pods per plant, mean across three seasons) were superior in pod set to II/95 and II/96 (1.5^{d}, mean across two seasons); the latter two did not significantly differ from each other.

Lema

Nodes. Plant growth in I/95 (43.3^{d}) and II/95 (37.4^{d}) was better than I/96 (27.1^{d}) and II/96 (24.2^{d}). I/97 (45.0^{d}) accounted for better developed plants than II/95, I/96, and II/96 ($F = 18.7^{**}$). The plants in NPK^{+} grew bigger, with 44.6^{d} nodes per plant on the average than those in NPK^{-} (26.4^{d}) ($F = 103.6^{**}$).

Flowers. Direct seasonal effects were not observed; they rather interacted with NPK fertilizer. NPK^{+} in I/96 (1.4^{d}) produced more flowers than all treatments (with and without fertilizer) in I/95, II/95, and II/96, all around 0.5^{d} flowers per plant ($F = 3.3^{*}$). I/96 under NPK^{+} also formed more flowers than I/97 in NPK^{+}. As for the flower index, season I/96 yielded a more favorable proportion of flowers to nodes than I/95, II/95, and I/97 ($F = 4.6^{*}$). All other seasons were similar to each other. Non-fertilized plots showed a better ratio over the ones treated with NPK ($F = 8.9^{**}$).

Pods. Pod formation was significantly higher in I/96 (3.5^{d} pods per plant) than in I/95 and II/95, both with 0.9^{d} pods ($F = 3.5^{*}$). Fewer pods were produced in I/95 on both NPK levels than on NPK^{+} in II/96 (1.8^{d}) and I/97 (2.9^{d}) ($F = 3.0^{*}$). The same patterns applied for both levels in II/95 in contrast to II/96 (3.2^{d}) (with NPK) and I/97 (without NPK). NPK^{+} in I/96 (3.8^{d}) produced more flowers than in I/97 (1.5^{d}). Within non-fertilized treatments, seasons I/95 and II/95 produced fewer pods than I/96 and I/97. When fertilized plots only were compared, seasons I/95 and II/95 were inferior to seasons I/96 and II/96, and season I/96 produced more pods than I/97.

IITA

Nodes. In II/96 plant size was smallest averaging 16.7 nodes per plant during the season ($F = 19.9^{**}$). I/95 (48.6) and II/95 (47.1) were similar, both deviating from I/96 (33.4), II/96 (16.7) and I/97 (35.4).

Flowers. Though producing equal numbers of flowers as I/97, II/96 (0.3^{d} flowers per plant) was inferior to I/95, II/95, and I/96 (0.9^{d}), which hardly deviated from each other ($F = 3.9^{*}$). Season I/96 had a significantly higher flower index than I/95, II/95, and I/97 ($F = 4.6^{*}$).

Pods. While I/97 (8.1^{d} pods per plant) formed about the same number of pods as I/95, counts were higher than I/96 (4.0^{d}), II/95 (1.8^{d}), and II/96 (0.9^{d}) ($F = 20.5^{**}$). I/95 and I/96 did not differ but were superior to II/95 and II/96. I/95, I/96, and I/97 on average had higher records than the mean of II/95 and II/96 in common.

Differences within seasons

Although the figures generally consist of letters a) to d), a) is not mentioned in the text. This part displays data on precipitation and serves as complement for the subsequent components of the figures.

Tokpa/Ayou

First season (I/95)

Nodes. No treatment effects were suggested by the analysis. However, the time main effect (DAP) (across treatments) fitted best to a quadratic trend ($F = 320.9^{[q]**}$) and marked the end of plant growth at DAP 70, indicated by a non-significant growth rate from DAPs 63 to 70.

Flowers. No significant influences by treatments occurred on trends and main effects. However, a slight deviation between the curves with and without NPK was visible (Fig. 2.5c.). At DAP 49, the seasonal peak (univariate ANOVA), where the profiles deviated most, the difference between NPK^{+} (5.2^{d} flowers per plant) and NPK^{-} (3.2^{d}) was significant using univariate ANOVA on a single time point ($F = 14.0^{**}$). However, since the trend did not show multivariate differences ("Hummel-Sligo procedure," Hummel & Sligo 1971; Barker & Barker 1984, p. 38), this has to be viewed with caution (Huberty & Morris 1989; Scheiner & Gurevitch 1993). Similar to findings for flowers were results on the flower index, which revealed higher profiles for fertilized plots over time (DAP). The variation was not significant (Fig. 2.5c.).

Pods. No impact of treatments on pod formation was found (Fig. 2.5d.).

Second season (II/95)

Nodes. Vegetative growth responded more positively to NPK application (37.8[d] nodes per plant) than to NPK^- (30.5[d]) ($F = 14.3^{**}$). This effect was also found in profiles, which developed distinctly from the beginning of counts (DAP 35), indicating a faster growth of plants in NPK^+ ($F = 5.6^{[l]**}$) (Fig. 2.6b.). The non-significant time effect indicated the end of vegetative growth from DAPs 63 to 70.

Flowers. Except for the time main effect (as to be expected), no impact due to treatments could be observed (Fig. 2.6c.). Peak of flowering occurred late at DAP 63. The flower index (across time) was higher in NPK^-, indicating a relatively higher number of flowers per vegetative mass than NPK^+ ($F = 5.6^{*}$) (Fig. 2.6c.).

Pods. Pod formation was not influenced by application of different treatments (Fig. 2.6d.).

Third season (I/96)

Nodes. Treatments under NPK^+ accumulated on average more vegetative mass (42.4[d] nodes per plant) than those without (34.1[d]) ($F = 18.9^{**}$). The profiles diverged over time right from the first counting event (DAP 28) in favor of NPK^+, which had about 16 nodes more (30%) at DAP 63 than NPK^- ($F = 5.1^{**}$) (Fig. 2.7b.). A mulch main effect was found favoring development in the control (42.2[d] nodes per plant) compared with a significantly lower level in *Senna* (37.0[d]) and *Imperata* (35.4[d]) ($F = 4.5^{*}$). From DAP 56 to DAP 63 plant growth almost came to a standstill as indicated by a non-significant time effect.

Flowers. The number of flowers produced was not influenced by treatments applied to the plots. DAP 49 displayed the highest flower counts (Fig. 2.7c.). Responses on the flower index were virtually equal, showing no impact of treatments (Fig. 2.7c.).

Pods. On plants in NPK^+ more pods developed in total (15.3[d] pods per plant) than the 11.7[d] pods under NPK^- ($F = 10.0^{**}$) (Fig. 2.7d.). More pods were counted in the control (15.3[d]) and under *Senna* (14.4[d]) in contrast to mulch of *Imperata* (11.0[d]) ($F = 5.7^{**}$). The control also scored higher than the two mulch types together. Pod numbers (across treatments) did not increase between DAPs 63 and 70.

Fourth season (II/96)

Nodes. Plants responded positively on NPK application, counting 32.3[d] nodes per plant with and 23.5[d] without fertilizer ($F = 20.8^{**}$). The trend in chemical fertilizer use emphasized the positive overall effect while significantly widening the gap between application and non-application ($15.16^{[l]**}$) (Fig. 2.8b.).

Flowers. Treatments did not have any impact on flower development (Fig. 2.8c.). Flower numbers peaked at DAP 56 and declined slowly, with flowers still appearing one week

before harvest (DAP 70). The flower index did not suggest differences in variation between treatments (Fig. 2.8c.).

Pods. The tendency towards higher pod formation in NPK^+ took effect remarkably on a quadratic trend ($F = 4.6^{**}$) (Fig. 2.8d.). Having reached DAP 63, pod development slowed for NPK^- while pod numbers dropped slightly for NPK^+.

Fifth season (I/97)

Nodes. Plants grew on average better in NPK^+ (64.6^d nodes per plant) than in NPK^- (48.9^d) ($F = 40.3^{**}$). Considering the mulch main effects, plants developed more vegetative mass in the control (60.8^d) in contrast to *Imperata* (52.7^d) ($F = 3.6^*$). *Senna* was in between. The assessment of profiles confirmed the results on the main effects. A wide gap divided the NPK profiles (Fig. 2.9b.) in favor of NPK^+, which increased slightly with time ($F = 2.8^{[l]*}$). Starting with a difference of about 10 nodes the gap doubled during the season. As for mulch profiles, the control plants reached the highest level of growth, rising only marginally more than plants under *Senna* but growing faster than those under *Imperata* ($F = 2.9^{[q]**}$). Plants with *Senna* mulch gained faster in size than those with *Imperata* over time. The control demonstrated a higher growth rate right from the beginning than mulch treatments together. As far as simple effects of NPK are concerned, no mulch differences were found within NPK^+ plots. Within non-fertilized plots, plants in the control grew faster than those in *Senna* and *Imperata* ($F = 4.5^{[q]**}$). Vegetative growth stopped after DAP 63.

Flowers. Numbers of flowers were found to deviate on NPK levels over time ($F = 5.5^{**}$). Trends were investigated but did not reveal any divergence on trends (linear, quadratic, cubic). The pattern of the graph (Fig. 2.9c.) suggested focusing on univariate differences on single DAPs. Since the multivariate interaction NPK by DAP was significant, protection against inflated type I error was assumed (Hummel & Sligo 1971; Barker & Barker 1984; Scheiner & Gurevitch 1993). On DAP 49 more flowers were counted for NPK^+ and later again on DAP 77. Flowering in NPK^- peaked at DAP 56 and scored higher than NPK^+. NPK^- delayed in flower onset, peaked (4.8^d flowers per plant) sooner and higher than NPK^+ (3.4^d), and declined towards the end of the season, falling below the levels for NPK^+ at DAP 77. Profile investigation uncovered differences on the flower index in the same pattern as for the numbers of flowers (Fig. 2.9c.). In contrast to flowers, where trends were not found to differ, index profiles deviated on the second order polynomial ($F = 17.4^{[q]**}$), leading to a higher peak for NPK^- at DAP 56, one week later than for NPK^+. The factor mulch exerted an influence on the flower to nodes ratio. The control revealed the lowest quotient, while *Imperata* scored highest ($F = 6.1^{**}$). The control was less favorable than mulch on the average. Assessing effects within NPK^- (simple effect), this effect was even stronger. Non-fertilized *Imperata* was superior in relative flower production to both *Senna* and the control ($F = 7.1^{**}$). In the same way mulch scored higher on average than the control. Within NPK^+, differences were not significant.

Pods. Pod numbers deviated on a mulch main effect where the control in general yielded the highest counts (14.7^{d} pods per plant) (F = 4.3*) (Fig. 2.9d.). This was significantly more than for *Senna*, which remained at the lowest level (12.4^{d}). The control produced still more than both mulch types together.

Lema

First season (I/95)

Nodes. A clear difference was observed between NPK^{+} with 51.5^{d} nodes per plant and NPK^{-} (35.7^{d}) (F = 28.9**). On the profiles for the same effect the gap widened continuously in favor of NPK^{+} (F = 5.6$^{[l]**}$) (Fig. 2.10b.). A sudden decline in numbers at DAP 56 seems to be due to an external impact like rodents, which might have attacked certain plants. Plants to be counted had to be changed later on.

Flowers. Numbers of flowers as well as the flower index did not vary between treatments (Fig. 2.10c.). When counting was started at DAP 42, numbers were already at the maximum, with flowering declining one week later.

Pods. Considerable variation due to treatments could not be detected (Fig. 2.10d.). From DAP 63 to DAP 70 in general the onset of new pods almost stopped as suggested by a non-significant time effect. Pod numbers peaked at DAP 56, being tendentiously higher for fertilized plots. Only one week later the numbers approached zero.

Second season (II/95)

Nodes. NPK^{+} strongly favored plant development to a mean size of 49^{d} nodes per plant over NPK^{-}, where plants remained small (27.4^{d}) (F = 36.9**). The trend of the profiles (Fig. 2.11b.) between NPK^{+} and NPK^{-} diverged increasingly with time (F = 11.8$^{[l]**}$). A sudden increase in NPK^{+} appeared at DAP 49.

Flowers. Treatments did not influence development of flowers. Highest flower numbers were counted at DAP 49 right at the beginning, but the numbers declined further on describing a linear trend (F = 37.6$^{[l]**}$) (Fig. 2.11c.). Relative flower production, which was calculated as the flower index, was more favorable on the trend during the season for NPK^{-} right from the beginning (DAP 49) (F = 2.9$^{[q]*}$) (Fig. 2.11c.). The obvious decrease of the index after DAP 49 happened in parallel with the abrupt increase in plant size.

Pods. Right from the beginning when pod counts began, the number – already very low – declined through the following counting events (Fig. 2.11d.). Whereas pod numbers in NPK^{-} decreased from two pods per plant to one pod on the average during three weeks, they dropped in NPK^{+} from almost four pods to nearly one (F = 4.3$^{[l]**}$). The first remarkable drop

in pod numbers for NPK^+ coincided with the sudden increase of vegetative mass from DAP 49 to DAP 56 (Fig. 2.11b.).

Third season (I/96)

Nodes. NPK exerted a strong influence on plant growth. Plants were bigger in NPK^+ with 42.8^d nodes per plant compared with NPK^-, where plants reached only about half this size (23.18^d) ($F = 139.4^{**}$). These findings came out more clearly by use of trends (Fig. 2.12b.). A linear trend divided NPK^+ markedly from NPK^- ($F = 31.0^{[l]**}$). Whereas plants in NPK^- grew comparatively slowly and came to their final size towards the end of the season (DAP 63), plants under NPK^+ developed fast and were still gaining vegetative mass at the end of the season.

Flowers. Flower development responded strongly to the application of fertilizer (Fig. 2.12c.). Fertilized plants produced significantly more flowers over time until DAP 56, with a distinct difference in peak at DAP 49 favoring NPK^+ ($F = 3.7^{[l]**}$). After DAP 63 a second increase in flower production for NPK^+ occurred. NPK application lead to a marked difference in the flower index on the trend ($F = 3.9^{[q]*}$) (Fig. 2.12c.). In relation to plant size, NPK^- had a more favorable quotient until DAP 56, falling below levels of NPK^+ at DAP 70.

Pods. The profiles for the NPK effect showed a significant difference ($F = 5.5^{**}$) (Fig. 2.12d.). Slightly higher numbers of pods for NPK^+ at DAP 49 were leveled the following two weeks by NPK^- when from DAP 63 on pod numbers increased markedly for NPK^+. At DAP 70 non-fertilized plots reached less than 60% of pod numbers obtained in fertilized treatments.

Fourth season (II/96)

Nodes. Plant size was superior under NPK^+ right from the onset of counts, with 31.7^d nodes per plant to the NPK^- average of 17.6^d nodes (Fig. 2.13b.) ($F = 71.8^{**}$). The profile for fertilized plots increased faster especially during the second half of the season ($F = 3.8^{[q]*}$).

Flowers. The use of fertilizer enhanced flower production over time and resulted in a higher peak at DAP 49 (3.2^d flowers per plant) joining the level for NPK^- afterwards (Fig. 2.13c.) ($F = 4.5^{[q]**}$). A marginal effect was found for mulch over time. Contrasts pointed to a possible variation between the control and *Imperata* ($P \geq 0.05$). *Imperata* produced fewer flowers but these stayed on for one more week whereas flowers in the control dropped immediately and fell below the level of *Imperata*.

Pods. The considerably higher flower production in NPK^+ led to more pods being formed in these treatments – 4.3^d pods per plant contrasting with 2.4^d pods for NPK^- (Fig. 2.13e.) ($F = 7.5^{**}$). The profile for NPK^+ increased strongly between DAPs 42 and 49 and remained more or less parallel to the one for NPK^- ($F = 8.5^{[q]**}$). Increase in pod production ceased after DAP 63 for both profiles.

At peak flowering (DAP 49), the flower index suggested about the same relative flower production between NPK levels, but whereas the trend for NPK^+ dropped immediately it remained higher for NPK^- (Fig. 2.13d.) ($F = 5.0^{[q]*}$).

Fifth season (I/97)

Nodes. As in the preceding seasons, vegetative mass development was favored by the application of NPK. NPK^+ averaged 57.8^d nodes per plant in contrast to NPK^- with 33.8^d nodes ($F = 38.4^{**}$). A visible difference in trends appeared after DAP 56, when NPK^+ rose steeply, widening the split with NPK^- (Fig. 2.14b.) ($F = 19.3^{**}$). Mulch also had an impact on plant growth over time leaving behind plants without mulch (control) ($F = 2.6^{[l]*}$). The control increased marginally slower than *Imperata* and stayed significantly behind the growth achieved in *Senna*. *Senna* also showed a steeper increase in size than *Imperata*. This was fitted on a first order polynomial.

Flowers. Main effects of NPK distinctly put non-fertilized plots in favor (0.9^d flowers per plant against 0.5^d for fertilized plots) as far as overall numbers of flowers are concerned ($F = 5.0^*$) (Fig. 2.14c.). A trend was not discovered. The flower index favored NPK^- with a significantly higher peak at DAP 49 ($F = 14.5^{**}$). The trend was marginally distinct for the NPK by time interaction after ANOVA, but suggested a clear difference in shape of the profile when polynomial contrasts were used ($F = 8.4^{[q]**}$) (Fig. 2.14d.). A steeper slope towards DAP 49 and a faster decrease after DAP 56 for NPK^- accounted for the effect. As far as mulch showed impact the control displayed a more favorable coefficient than mulch ($F = 3.8^*$). When compared separately, the control was higher than *Imperata*.

Pods. NPK exerted a visible influence on pod formation ($F = 6.7^*$). NPK^- (2.9^d pods per plant) produced in total (across time) twice as many pods as NPK^+ (1.5^d). The profiles marginally differed in trend in favor of NPK^- (Fig. 2.14e.), but this was not significant. Mulch had an impact, too ($F = 6.6^{**}$). The control yielded more pods during counts than mulch (*Senna*, *Imperata*). No differences in slopes were recognized among treatments. Pod onset came to a standstill after DAP 70.

IITA

First season (I/95)

Nodes. On the mulch main effects the control was close to neem (39.5^d nodes per plant), but plants were significantly smaller than in *Imperata* and *Senna* (46.4^d) ($F = 9.4^{**}$) (Fig. 2.15b.). Plant development ceased after DAP 56.

Flowers. Differences in flower development and on the flower index due to treatments were not revealed. Peak flowering was at DAP 49, where *Imperata* suggested a slightly higher level (Fig. 2.15c.).

Pods. Pod numbers in the control (11.4^{d} pods per plant) and *Imperata* were close together and varied significantly from neem (14.1^{d}) and *Senna* (14.4^{d}) on the main effect, both superior in counts ($F = 6.6^{**}$) (Fig. 2.15e.). DAP 56 was marked as the end of further increase of pod numbers.

Second season (II/95)

Nodes. After ANOVA, marginal influences were reported among the mulches ($P \geq 0.05$). Neem was suggested as having developed bigger plants (49^{d} nodes per plant) than *Senna* (38.3^{d}). Plant size did not increase after DAP 56 due to a non-significant time effect (Fig. 2.16b.).

Flowers. Flower development and the flower index could not be influenced by mulch. However, neem tendentiously remained on a slightly lower level of flower production. Its peak occurred at DAP 49 (Fig. 2.16c.). At DAP 56 there was a short setback in the control.

Pods. Deviations among treatments were not found, the overall mean being 3.4^{d} pods per plant at DAP 70. The trend in lower flower numbers resulted in weaker pod set. After DAP 56 no additional pods were formed (Fig. 2.16e.).

Third season (I/96)

Nodes. Plant growth was different (across time) between *Senna* with 27.2^{d} nodes per plant and *Imperata*, which was superior on average (31.9^{d}) ($F = 3.2^{*}$). After DAP 56 no increase in number of nodes was counted (Fig. 2.17b.).

Flowers. Flower production had its maximum at DAP 49. Differences due to treatments did not occur across time. In terms of the peak in a univariate type of analysis, neem had significantly more flowers (8.1^{d} flowers per plant) than the control (3.4^{d}) on this single event ($F = 4.9^{*}$) (Fig. 2.17c.). However, this finding is not supported by overall significant results and has to be regarded with caution (Huberty & Morris 1989). Neem showed the highest flower index and was significantly distinct from the control on the mulch profile ($F = 2.8^{[q]*}$) (Fig. 2.17d.).

Pods. The control yielded highest pod counts (15.3^{d} pods per plant) compared with mulch in general ($F = 7.3^{**}$). *Senna* with 9.3^{d} pods remained below the control, *Imperata* had 12.9^{d}, and neem had 12.8^{d}. Pod formation stopped after DAP 56 (Fig. 2.17e.).

Fourth season (II/96)

Nodes. A slight but non-significant variation due to mulch was found, which suggested that *Senna* produced the biggest plants (17.6^{d} nodes per plant), being superior to the control

(15.4[d]) and *Imperata* (15.1[d]). After DAP 49 no increase in growth was recorded for the control and neem, whereas *Imperata* and *Senna* still gained vegetative mass (Fig. 2.18b.).

Flowers. Flowering peaked relatively late at DAP 56, showing no sign of mulch impact (Fig. 2.18c.). This was the same for the flower index (Fig. 2.18d.). Flower numbers were low in general.

Pods. Mulch types had a significant impact on the number of pods formed across time on the plants. *Senna* produced the most pods (2.5[d] pods per plant) ($F = 10.5^{**}$). In turn *Imperata* came off badly with 0.8[d] pods only and was inferior to all the other treatments. Pod formation ended after DAP 63 (Fig. 2.18e.).

Fifth season (I/97)

Nodes. On the main effects across time the control had on average fewer nodes (30.4[d] nodes per plant) than *Senna, Imperata,* and neem (37.5[d]); these three were almost equal in number ($F = 11.9^{**}$) (Fig. 2.19b.). After DAP 49 the increase rate for plant growth approached zero.

Flowers. Mulch was found to interact with time for differences on the trend but neither first nor second polynomial fitted to reveal deviations in level or shape of the profiles (Fig. 2.19c.) ($F = 2.1^{*}$). Univariate analysis was used to explain those interactions. For DAP 49 the control was lowest (2.3[d] flowers per plant), deviating from neem and *Imperata*. *Imperata* (4.6[d]) was significantly higher than *Senna* ($F = 18.54^{**}$). *Senna* excelled *Imperata* one week later at DAP 56 and was still superior to neem on DAP 63 at an already very low level. *Imperata* and neem peaked at DAP 49, whereas the control and *Senna* rose to their maximum one week later. However, the univariate results have to be regarded with caution as they are not protected by multivariate significance (Huberty & Morris 1989; Scheiner & Gurevitch 1993). The flower index showed similar results to the total flower production (Fig. 2.19d.). Again, the interaction of mulch on time could not be fitted to polynomials of first or second order. However, this marginal effect was not significant. A univariate approach was used for further investigation. On DAP 49 *Imperata* seemed to have a better ratio than neem, *Senna,* and the control. An inverse effect was noticed for DAP 56, where *Imperata* scored lower than the control. However, significance was not found.

Pods. *Imperata* yielded the highest pod counts across time with 9.8[d] pods per plant; this was superior to neem (8.7[d]), the control, and *Senna* (7.0[d]), the last two hardly differing from each other ($F = 22.4^{**}$) (Fig. 2.19e.). Neem also was better in results than the control and *Senna*. After DAP 56, pod formation leveled out indicating the end of reproductive growth.

Discussion

Regional differences

All regions

Nodes. Plants remained significantly smallest in season II/96 and were only slightly better developed in season I/96 (Table 2.8.). Across the three regions, precipitation was much lower in season II/96 compared with all other seasons and was possibly a limiting factor. Drought stress reduces leaf area and limits dry matter production (Turk & Hall 1980b; Wien & Summerfield 1984) since performance of symbiotic nitrogen fixation through nodules depends on soil humidity (Summerfield et al. 1974). Fertilizer treatments on the other hand could not compensate for low nodulation as applied nutrients dissolve slowly in the soil. At IITA and in Lema rains ceased completely after DAP 42, whereas in Tokpa/Ayou they continued until pod formation (Tables 2.2., 2.4., 2.6.). Phosphate contents in depths up to 60 cm were lower in season II/96 and possibly reduced the plants' potential for nodulation, which is strongly influenced by accessibility of this element in the soil (Tewari 1965; Rachie & Roberts 1974; Summerfield et al. 1974; Cadisch et al. 1989; Giller et al. 1998). In this context a generally lower nitrogen level, which was measured in season II/96, possibly reduced protein synthesis and chlorophyll content (Finck 1969), although cowpea does grow at relatively low fertility levels (Sellshop 1962; Summerfield & Roberts 1983; Summerfield et al. 1983) and shows almost no effects of nitrogen application on well-nodulated plants (Rachie & Roberts 1974; Duke 1983; Wien & Summerfield 1984). The plants probably compensated for limited nitrogen access in the soil by mobilizing nitrogen from the leaves, leading to a faster senescence of the plant and implying reduced vegetative growth (Summerfield et al. 1983) caused by "self-destruction" (Sinclair & de Wit 1975, 1976) of the plants. Potassium levels, too, were low, particularly in the lower soil layer (10-60 cm), where most of the root biomass allegedly was dispersed due to dry conditions. Plants cultivated under lower potassium levels are more susceptible to drought stress (Finck 1969). Soil carbon contents were slightly lower in this season compared with the others. Lema recorded better developed plants than IITA in season II/96, which possibly can be explained by double the amount of rainfall combined with higher potassium and pH levels in Lema than at IITA. Results for plant development in season I/96 were hardly better than for II/96 although I/96 revealed highest rainfall over all five seasons in Lema and at IITA. Reduced levels of phosphate and carbon in the lower soil stratum in I/96 and less nitrogen in the upper layer (0-10 cm) possibly accounted for this. In season I/97, where Tokpa/Ayou developed the biggest plants, levels of cation exchange capacity, carbon, nitrogen, and magnesium were more elevated than in the other regions (Table 2.1.). Increased magnesium levels are

principally important for photosynthesis as an element of chlorophyll and protein synthesis (Vogel & Angermann 1967; Finck 1969). The combination of higher nitrogen supply and an improved cation exchange capacity, which serves as nutrient storage system (Müller-Sämann & Kotschi 1997), favored plant growth on the basis of relatively high precipitation in this season (Tables 2.2., 2.4., 2.6.).

Flowers. Season I/96 reached overall highest flower counts while insect counts of thrips, which were carried out in parallel, resulted in relatively late population peaks in all three regions, allowing an undisturbed flowering at the beginning of the season. Thrips numbers before these peaks were relatively low since continuous precipitation at Tokpa/Ayou and at IITA until DAP 49 did not favor a population build-up of thrips in flowers. Additionally, potential alternative host plants were not found at Lema or at IITA in the vicinity of the cowpea fields (Figs. 7.10., 7.14.) and only one species occurred in Tokpa/Ayou (Fig. 7.4.) from which a steady migration into cowpea could be expected. In contrast, season II/96 yielded the lowest flower counts, which conceivably was caused by comparatively higher thrips abundance in flowers and environmental stress due to low precipitation as well as nutritional limits, which were formulated for plant growth above. The low flower numbers during season I/95 in Lema compared with both other regions might be explained mainly by lower phosphate, carbon, nitrogen, and magnesium levels in this region (Table 2.1.), accounting for important functions like protein synthesis, enzyme activation, and chlorophyll content (Vogel & Angermann 1967; Finck 1969). Insect damage causing considerable flower shedding can be excluded since insect abundance levels were low compared with the other regions (Table 3.2.), peaking late at DAP 63 when the main flowering period came to an end. In turn, the better growth conditions of plants and the superior flower output in Tokpa/Ayou during season I/97 followed a better supply of nutrients on the basis of cation exchange capacity, carbon, nitrogen, and magnesium, which supposedly accounted for this effect. The fact that generally lower flower numbers were counted during the late growing seasons compared with early seasons can be explained principally by the much higher thrips abundance in late seasons, which remarkably outnumbered those of early seasons and caused more flower shedding (Taylor 1964; Wien & Tayo 1979; Tamò et al. 1993b; van de Klashorst & Tamò 1995).

Flower index. Season I/96 resulted in the most favorable index because the plants were relatively small (Table 2.8.), but yielded the highest flower counts over all other seasons (Table 2.9.). Developing much better in season I/97, plants also yielded a higher flower number on average, leading to a more favorable flower ratio per nodes; this contrasts with season II/96, which resulted in most detrimental flower onset. The fact that in season II/96 plants in Lema developed highest vegetative mass compared with the other regions (Table 2.8.) and had about the same flower production as Tokpa/Ayou (Table 2.9.) would suggest a lower index for Lema compared with Tokpa/Ayou; in fact, the opposite was found by analysis. Since counting of nodes was suspended after DAP 56 the index could be used until this sampling day only although flowering still continued. Between DAP 35 and DAP 56, where the index could be

applied, Lema in fact produced more flowers than Tokpa/Ayou and led to a higher index. The results from analysis are therefore correct. Whereas flower production dropped remarkably in Lema after DAP 56 but continued on higher levels in Tokpa/Ayou, the overall flower numbers were marginally higher in Tokpa/Ayou than Lema (Table 2.9.). This flower index cannot be used as estimator for later yield estimates because plant growth (number of nodes) of the indeterminate growth type at flowering has little consequences for subsequent economic yield (Wien & Summerfield 1984). The cowpea variety used is known to be semi-determinate, but developed rather indeterminate-like under humid conditions and approached a determinate habitus during the dryer late seasons. This index rather served as an indicator describing if the plants tended towards vegetative mass production or emphasized reproductive output.

Pods. Differences in flowering did not always correspond with the differences in pod formation. The variation in flower production between seasons I/96 and I/97 was minimized at pod formation stage. The initially higher flower numbers in season I/96 did not produce more pods compared with season I/97. During the growing cycle of cowpea 70-88% of all flowers produced are shed naturally (Inoue 1955; Ojehomon 1972; Rachie & Roberts 1974; Wien & Summerfield 1984), and the more flowers open the more they are shed (Ojehomon 1968). Thus, the comparatively high flower numbers in season I/96 could not be maintained until maturity. A higher soil fertility level would be necessary to satisfy the strong demands of these major sinks for basic elements, which obviously was not the case (Table 2.1.). Additionally, higher precipitation during season I/96 at least in Lema and IITA possibly caused more losses due to unidentified pod rot. This phenomenon was strongest in Lema. The abundance of thrips could not explain this effect since their levels were similar in seasons I/96 and I/97. Differences in pod numbers for seasons I/95 and II/96 were straightforward results of flower numbers in the respective seasons. Flower numbers in season I/96 did not reveal significant differences between regions, but Tokpa/Ayou in total counted significantly more pods than Lema. Although the principal nutritional elements were lower in soils in Lema, the amount of phosphate was 1.6 times higher than in Tokpa/Ayou. This comparatively high level might have suppressed fruit set (Wien & Summerfield 1984). In addition, pod losses through decay may have been higher in Lema, which recorded about 130 mm more precipitation during this season than Tokpa/Ayou (Tables 2.2., 2.4.). A similar effect was found in season I/97 between IITA and Lema. Despite marginally more flowers in Lema, more pods were counted at IITA. Phosphate levels were higher at IITA, possibly ameliorating nutritional conditions of the plant with subsequently increasing nodulation (Tewari 1965; Summerfield et al. 1974). During this season thrips abundance was obviously higher in Lema (Table 3.2.). Thus, although counts revealed slightly higher numbers in Lema, the comparatively higher thrips pressure probably lead to increased shedding after these flowers had been counted, eventually resulting in lower numbers. The significantly bigger plants in Lema (Table 2.8.) might have created a more humid microclimate generally closing the space between rows in a roof-like manner. This could have led to a comparatively higher loss through rot. The pattern that occurred for flower counts among

early and late seasons, also applied for pod numbers in the same way. The generally lower pod set during late seasons can be explained mainly by twice as heavy thrips abundance in these seasons, which considerably increased the numbers of flower buds and flowers being shed and lost as reproductive organs (Wien & Tayo 1979). In addition, the premature loss of pods due to hastened dry-off under drought conditions in late seasons was stronger than any losses caused by rot under wet conditions at the end of early seasons. Such losses were difficult to estimate, however.

On-farm regions

Nodes. Plants were generally bigger in treatments where NPK fertilizer was applied. This response is directly attributable to the increase of nitrogen, phosphate, potassium, and magnesium, which are of vital importance for the vegetative development of plants (Sellshop 1962; Tewari 1965; Finck 1969; Summerfield et al. 1974; Giller et al. 1998). A consideration of the simple effects within non-fertilized plants showed that Tokpa/Ayou always exhibited more vegetative mass than Lema in parallel to the qualitative results on soil nutrients (Table 2.1.), which generally revealed higher levels of cation exchange capacity, nitrogen, magnesium, and, except for seasons I/96 and II/96, phosphate. In turn, potassium levels generally were more elevated in Lema. In terms of fertilized treatments only, plants were marginally better developed in Lema compared with Tokpa/Ayou although this was not of significant importance. The response to fertilizer thus was stronger in Lema than Tokpa/Ayou. At Tokpa/Ayou, the higher cation exchange capacity – that is the soil's capacity to store nutrients (Müller-Sämann & Kotschi 1997) – favored plant growth in combination with generally higher levels of main nutritive elements. This was visible in the non-fertilized plots. Since nutrients were supplied by fertilizer, the relatively poor soils in Lema became temporarily fertile enough for similar vegetative development as in Tokpa/Ayou. The always lower carbon content, indicating less humus in the soils, together with much lower nitrogen in Lema can be attributed to the regular burning during the long dry season in this savanna region. Burning incurs the loss of carbon and nitrogen, which is the main reason for the savanna's overall deficits of these nutrients (Charreau 1974, cited in Balasubramanian & Nnadi 1980; Müller-Sämann & Kotschi 1997). The higher potassium content of soils in Lema might be due mainly to yearly burning in the long dry season as the name "potash" suggests (Finck 1969).

Flowers and Pods. Although after application of fertilizer, especially the element phosphorus, an increase in flower production would be expected, leading to more pods (Giller et al. 1998), no significant variation was observed between fertilized and non-fertilized plots. On the other hand, the anticipated increase in pest abundance through fertilizer (Bentz et al. 1996) was confirmed. A significantly higher abundance of *Maruca vitrata* and an at least marginally higher population of thrips, which were observed in parallel, apparently compensated for this expected effect through higher flower shedding in fertilized treatments.

Flower index. The ratio of flower number to plant size emphasized the overall higher production of vegetative mass after fertilizer application, which did not lead to an increase in generative response. Fertilized plants develop a rather unnecessary size, with soft tissue that is more susceptible to insect attacks (Finck 1969; Bentz et al. 1996; Mollema & Cole 1996). The decreasing index due to greater vegetative mass caused by use of fertilizer, combined with a more or less unchanged flower output, might be the result of the generally lower performance of leguminous plants in nitrogen and phosphate-rich soils (234 kg NPK per hectare were applied, being equivalent to 33 kg nitrogen per hectare and 54 kg phosphate per hectare) (Finck 1969; Rachie & Roberts 1974; Summerfield et al. 1978; Wien & Summerfield 1984). This reduced performance after NPK application could be caused by the known antagonism between nitrogen and phosphorus based on ion concurrence. Increasing nitrogen supply reduces the uptake of phosphorus, but nitrogen uptake is not influenced by phosphorus levels (Finck 1969). Thus nitrogen effects on plant development are expected to dominate if NPK is applied, more so because a certain quantity of phosphorus becomes directly fixed to complexes in the soil. Furthermore, flower numbers were reduced through increased attacks by insects, which are attracted by higher nitrogen levels in plants (Bentz et al. 1996; Mollema & Cole 1996).

Seasonal differences within the same region

Tokpa/Ayou

Nodes. Plants developed best in season I/97, possibly due to the higher amount of rainfall compared with the other seasons. Comparatively higher levels of carbon and magnesium in both soil strata probably strengthened this effect (Table 2.1.). Plant development in season I/95 was better than the remaining seasons II/95, I/96, and II/96 accompanied by results of higher cation exchange capacity (CEC), phosphate, pH, carbon, and potassium levels. The better availability of nutrients (CEC) (Müller-Sämann & Kotschi 1997) and the slightly higher levels of these elements could have favored plant size. The unfavorable vegetative plant development in season II/96 is attributable to lower rainfall and less of phosphate, carbon, nitrogen, and potassium in both soil layers. The obviously lower potassium levels (Table 2.1.), exacerbated the by insufficient precipitation, induced drought stress (Table 2.2.) since this element is known to economize water consumption of plants (Finck 1969). The limited dry matter production under dry conditions (Turk & Hall 1980b; Wien & Summerfield 1984), which limits nodulation and the symbiotic performance (Summerfield et al. 1974), and the reduced dilution of nutrients in fertilized plots seem principally responsible for reduced plant growth. The counts of missing plants, which recorded remarkably high losses in this season, confirm these conditions of stress.

Flowers. The clustering of flower numbers into early and late growing seasons, which were distinct within years but not among years, suggests a main influence of thrips attacks being much higher in later seasons and causing much more damage. Precipitation, too, was higher in all first cropping seasons, allowing overall more flowers on generally bigger plants.

Flower index. The significantly smallest plants in season I/96 and in turn the significantly highest flower numbers produced the most favorable index of generative per vegetative mass. Apart from that, higher indexes for all early seasons indicated better exploitation of potential reproductive resources on a given vegetative size, enhanced by higher precipitation and considerably lower pest abundance.

Pods. The clustering observed for flowers also applied directly for pods. The only exception was season I/96, which did not show significant differences from season I/97 in flower counts but at the end counted fewer pods than season I/97. Since insect attacks were less in season I/96 compared with I/97 and precipitation was lower, neither attacks by thrips nor humidity-induced rot could explain this undefined loss. The 120 mm lower precipitation in season I/96, given a flower number similar to season I/97, possibly was not enough to maintain the produced flower set until pod formation. Plants may have faced a higher natural flower shedding due to less favorable humidity conditions (Inoue 1955; Ojehomon 1972; Rachie & Roberts 1974; Wien & Summerfield 1984). Ojehomon (1968) states that as a rule more flowers are naturally shed the more of them are open.

Lema

Nodes. Seasons I/96 and II/96 resulted in the smallest plants (Table 2.8.), where in parallel the cation exchange capacity, carbon, nitrogen, and magnesium contents in the soil revealed lower values than for seasons I/95, II/95, and I/97 (Table 2.1.). Lower values for CEC and carbon reduced the soil's capacity to store nutrients (Müller-Sämann & Kotschi 1997) and the comparatively lower availability of nitrogen and magnesium, which are vital elements for protein synthesis, were likely limiting conditions for plant growth (Finck 1969). Precipitation was not thought to play a role since season I/96 recorded maximum rainfall and season II/96 had lowest amounts without resulting in considerable change in plant growth. The use of NPK fertilizer showed a clear effect across seasons attributable to the promoting influence of these elements on plant growth (Sellshop 1962; Tewari 1965; Finck 1969; Summerfield et al. 1974; Giller et al. 1998).

Flowers. Comparatively higher phosphate contents in the soil in season I/96 (Table 2.1.) favored the significantly higher flower production in this season (Table 2.9.). Phosphate is important for the reproductive phase (Finck 1969). Before sowing, the fields were cleared from a fallow lasting from two to over five years in the different replications, which might have accumulated nutrients, especially phosphate, and humus, which is known to store nutrients (Finck

1969; Müller-Sämann & Kotschi 1997). Additionally, thrips abundance remained relatively lower in season I/96 (Table 3.8.), possibly accounting for less flower shedding.

Flower index. By far the highest flower numbers were in season I/96 (Table 2.9.), and comparatively small plants (Table 2.8.) led to the most favorable index. Non-fertilized plots generally revealed a better index than fertilized ones. Both findings point to a better ratio of generative output on a given plant size. The larvae of thrips are considered as causing fourfold more damage to flowers (Tamò et al. 1993b), but adults were slightly more abundant in fertilized treatments, although not significantly so, suggesting the higher loss of flowers. A mainly nutritional preference of pests for better nourished plants (Bentz et al. 1996; Mollema & Cole 1996) could be the origin of this ratio.

Pods. Differences between season I/96 and contrasting seasons I/95, II/95, and I/97 followed straightforwardly from patterns in flower numbers. Seasons I/95 and II/95 had slightly lower flower numbers than season I/97, although not significantly so. These differences became significant for pods, the output of which was more favorable in season I/97. Since pest abundance was lower in seasons I/95 and II/95, though not accounting for higher losses, and precipitation was lowest in season II/96 but highest in season I/97, these effects could not explain the existing seasonal variation. Except for higher levels of magnesium in both soil strata in season I/97, no patterns were found in nutritional elements, which suggested an explanation. Although magnesium is important for chlorophyll and protein synthesis, its sole influence was believed to be too weak for the underlying results; this is consistent with the findings of Summerfield et al. (1974), who could not find a response to this element by vegetative growth or seed yield.

IITA

Nodes. The plants in season II/96 remained smaller than all other seasons. Phosphate and potassium levels were at the lowest levels (Table 2.1.), and precipitation was extremely low – not even reaching 100 mm from one week before sowing until DAP 77 (Table 2.6.). Mobilization of phosphate is reduced under drier conditions (Finck 1969) and the existing drought stress was worsened by comparatively low potassium levels, which led to reduced drought resistance of plants (Vogel & Angermann 1967; Finck 1969). The implications for dry matter production by drought stress, which were reported by Summerfield et al. 1974, Turk & Hall (1980b), and Wien & Summerfield (1984), are suggested as major reasons for the small plant size. During seasons I/95 and II/95 plants developed better than in seasons I/96, II/96, and I/97, without any sign of a respective variation in nutrient contents of the soils or patterns in precipitation. Thrips abundance was also higher in seasons I/95 and II/95. Since thrips attacks reduce flower numbers (Taylor 1964; Wien & Tayo 1979; Tamò et al. 1993b; van de Klashorst & Tamò 1995), the reduced sink represented by flowers might have reallocated nutrients into vegetative mass, indirectly compensating through loss in reproductive organs (Tamò, pers.

comm.). Wien & Tayo (1979) stated that cowpea is generally able to compensate for losses in vegetative or reproductive tissue. Lawrie & Wheeler (1974) found that flower removal, in this particular case through thrips attacks, causes a decline in nitrogenase activity and abnormal growth, which supports the hypothesis developed above.

Flowers. The cluster consisting of seasons I/95, II/95, and I/96 produced distinctly more flowers than seasons II/96 and I/97 (Table 2.9.). This happened in parallel with higher potassium levels in both soil strata for the first cluster and better phosphate supply for seasons I/95 and I/96 than II/96 (Table 2.1.). This effect appeared despite the higher abundance of adult thrips in seasons with more flowers (Table 3.2.). Since adults prefer to feed on pollen rather than on plant tissue (Tamò et al. 1993b), their damage potential was regarded as being minor despite their numbers. The better flowering performance of the plants allegedly could carry more thrips than plants in seasons II/96 and I/97. Season II/95, which had significantly higher larval densities, probably could maintain its comparatively high flower numbers due to the most elevated phosphate content in both soil strata. In turn, season I/97 remained lowest although precipitation was second highest among seasons and soil acidity was strongest (Table 2.1.). These were the lowest pH levels ever measured during all seasons in all regions. Low pH can fix micronutrients like molybdenum, which are important for plant development and productivity (Sellshop 1962; Rachie & Roberts 1974).

Flower index. The highest flower index occurred in season I/96, when the most flowers were produced. As plants remained at the second-lowest rank compared with the remaining seasons, the quotient resulted in lowest values. This indicated that higher flower production was possible per vegetative mass.

Pods. As far as seasons I/95, I/96, and II/96 are concerned, pod production followed straightforwardly from flowering patterns. Although having the lowest flower numbers, season I/97 resulted in highest pod output (Table 2.10.). Since the abundance of thrips larvae and adults was lowest in this season (Table 3.2.), very low flower shedding possibly led to most of the flowers produced turning into pods. The contrary was observed for season II/95, when high flower numbers were counted along with the highest thrips abundance, resulting in the second lowest pod results. A high flower count does not guarantee a similarly high pod count. It is likely that a large number of flowers fell off after counting due to the high thrips pressure (Taylor 1964; Wien & Tayo 1979; Tamò et al. 1993b; van de Klashorst & Tamò 1995). This additional external stress possibly helped the phenomenon of high natural flower and fruit loss (Ojehomon 1972; Rachie & Roberts 1974; Wien & Summerfield 1984), which is more accentuated the more open flowers and subsequently maturing pods appear (Ojehomon 1968).

Differences within seasons

Tokpa/Ayou

Nodes. In all seasons plants always developed better in the fertilized plots (Tables 2.5.-2.9.). Whereas the difference was marginal in season I/95, in all the other seasons it was significant. The NPK effects during seasons II/95-II/96 were distinct on levels (across time) as well as on trends. The direct nutritional advantages of fertilized plants, which were stated by Sellshop (1962), Tewari (1965), Summerfield et al. (1974), and Rachie & Roberts (1974), showed obvious effects. The difference in levels indicated a generally better response in fertilized plots. The positive trend for fertilizer plots showed the steady dissolution of applied nutrients, the uptake of which increasingly favored protein synthesis.

These results confirm findings by Sellshop (1962), who observed that highly fertile soils produce high yields of vegetative mass. Additionally, seasons I/96 and I/97 recorded bigger plants in the control compared with both mulch types. These findings oppose results of Masefield (1957), Terada (1971), Kamara (1980), Schoningh (1985), Remison & Mgbeze (1987), Daisley et al. (1988), Yih & Vandermeer (1988), Gupta & Rao (1989), Salau et al. (1992), Owino et al. (1993), and Adetunji (1994), who commonly agreed on increased vegetative development under mulch in cowpea and other plants. In parallel, both seasons revealed highest amounts of precipitation compared with the other seasons. Sandhu et al. (1992) observed in dryland wheat that mulch resulted in a significant positive response only in years with low rainfall during vegetative growth. Particular patterns in soil nutrients could not explain this phenomenon. Both seasons accumulated highest rainfall patterns, and rainfall means more clouds leading to reduced insolation. Unmulched plots possibly dried up earlier, allowing for a slightly higher soil temperature after the high amount of rainfall in both seasons, an advantage that might have slightly favored plant growth. Season I/97 was recorded as the significantly coolest season, and I/96 was not much warmer. Littleton et al. (1979a) reported that leaf area index increases more quickly during warm seasons; this effect has also been found by Njoku (1959), Wienk (1963), Ezedinma (1964), and Dart & Mercer (1965).

Plant growth in seasons I/95 and II/95 stopped after DAP 70, whereas it came to an end one week earlier in seasons I/96 and I/97 despite higher amounts of rainfall. In season II/96 counting was suspended before plant growth stopped. Non-fertilized, nodulated plants possibly had reduced nodulation due to lower temperatures in seasons I/96 and I/97 and stopped their development earlier than in the other seasons. Nitrogen supply inhibits symbiotic fixation while suppressing nodulation (Ezedinma 1964; Summerfield et al. 1977; Summerfield et al. 1978; Wien & Summerfield 1984). Nitrogen-dependent plants (fertilized) therefore did not set nodules effectively and stopped growing earlier, probably because of high leaching in these seasons strongly reduced the necessary chemical nutrient supply.

Flowers. Multivariate comparisons did not reveal treatment differences among fertilizer plots or mulch types in all seasons. A univariate test at DAP 49 in season I/95 marked higher flower numbers in fertilized treatments. Since the thrips population peaked two weeks later than the flower peak and remained at low levels around this time, chemically fertilized plants could fully exploit their nutritional advantages but they reached senescence faster while flower numbers dropped more quickly than the nodulated non-fertilized plants. If nitrogen is applied, symbiotic fixation is reduced and the plants' resources may not be used fully when leaves and roots age (Summerfield et al. 1978; Wien & Tayo 1979). In season I/97 fertilized plants started flowering in slightly higher numbers, but non-fertilized plants peaked higher one week later. Again, fertilized plants may have quickly used the applied nutrients, which suppressed nodulation subsequently (Summerfield et al. 1978), but high precipitation deprived them from further access by high leaching thus reducing further performance. In turn, non-fertilized plants could nodulate effectively and develop, although more slowly, higher performance, which lasted longer while permitting longer nutrient access through fixation (Summerfield et al. 1978).

Thrips numbers during these two weeks were low and can be excluded as an influencing factor (Fig. 3.5.). In seasons I/95 and I/96 peak flowering occurred at DAP 49 while thrips population established late towards DAP 63. Flowering was undisturbed by thrips attacks. Flower peaks in season II/95 were very late at DAP 63. Until DAP 35 precipitation was very low (Table 2.2.), retarding plant growth (Fig. 2.6.). Around the time of normal flowering (DAP 42) the amount of rainfall increased, keeping plant growth in vegetative development. When rains ceased at DAP 63, plants went into the reproductive phase with its flower peak. At the same time, adult thrips abundance peaked but due to their feeding habits mainly on pollen (Tamò et al. 1993b), their influence was considered less important. Generally low and – right after the peak – decreasing flower numbers did not offer favorable conditions for high oviposition, resulting in overall low larval thrips numbers (Table 3.2.). Flower peaks in seasons II/96 and I/97 at DAP 56 happened mostly undisturbed by thrips attacks, with larval numbers being highest at DAP 63. Whereas in season II/96 peak precipitation at DAP 49 possibly retarded the switch into the reproductive phase, high rainfall in the middle of season I/97 also increased vegetative growth and postponed flower set.

Flower index. Seasons I/96 and II/96 did not reveal differences in relative flower set. Bigger plants in season I/96 after NPK application showing no differences in flower numbers expressed an at least optically lower index for fertilizer plots, the difference of which was not significant. Since fertilized plants in season II/96 were significantly better developed and also produced slightly more flowers, the index almost leveled off between fertilized and non-fertilized treatments. In season I/95 a marginal advantage of fertilized treatments in terms of relative flower set was observed since plants associated with NPK application produced slightly more vegetative mass and peaked higher in flower numbers, producing a higher index. During seasons II/95 and I/97 the relative flower set turned out to be more favorable for non-fertilized treatments since in both seasons plants were significantly inferior in size and recorded

more flowers than the fertilized plots. In addition to this fertilizer effect in season I/97, mulch revealed a higher index than the control, reflecting more vegetative mass in the control but marginally the lowest flower set.

Pods. Seasons I/95 and II/95 did not show responses to treatments in the same way as the respective flower numbers were not different. The graphically displayed tendency (Fig. 2.5.) of slightly more pods in fertilized plots for season I/95 was the result of the higher flower peak at DAP 49 in the same treatment. Pod numbers in seasons I/96 and II/96 showed clear positive responses to fertilizer application without a significant effect on flower numbers. This was obviously because fertilized plants were bigger (number of nodes) given no differences in flower numbers. Their phenological potential (Summerfield et al. 1983; Summerfield & Roberts 1983) was higher, being the number of reproductive nodes associated with the total number of flowers, which has large effects on economic yield. Seasons I/96 and I/97 resulted in better pod set in the control compared with mulch, also given no differences in flower numbers. Again, this effect was a result of vegetative development (number of nodes), which followed the same patterns. The carrying capacity as phenological potential (Summerfield et al. 1983; Summerfield & Roberts 1983) led in total to more pods per plant.

Lema

Nodes. NPK led to distinct positive responses in vegetative growth in all seasons. The promoting influence was due to the applied nutrients phosphate, nitrogen, and potassium, and perhaps marginally to magnesium, which is vital for plant growth (Sellshop 1962; Tewari 1965; Vogel & Angermann 1967; Finck 1969; Summerfield et al. 1974; Giller et al. 1998). In season I/97, both mulch types produced bigger plants than the control. These results are confirmed by Masefield (1957), Terada (1971), Kamara (1980), Schoningh (1985), Remison & Mgbeze (1987), Daisley et al. (1988), Yih & Vandermeer (1988), Gupta & Rao (1989), Salau et al. (1992), Owino et al. (1993), and Adetunji (1994), who found that vegetative development increases under mulch in cowpea and other plants caused by improved soil humidity, higher nodule numbers and nitrogenase activity, more efficient water use, and increased pore volume, hydraulic conductivity, and earthworm and microbial activity, as well as cation exchange capacity, which assists in storing nutrients in the soil system (Müller-Sämann & Kotschi 1997).

Flowers. Treatment differences were not observed during seasons I/95 and II/95. In season I/95 flower maximum occurred at DAP 49, the first counting date for flowers. One week later the numbers had dropped markedly to about one flower per plant, which probably reflected increased shedding due to increasing numbers of thrips larvae between DAPs 42 and 49 although the abundance was not very high (Fig. 2.6.). About the same patterns prevailed in season II/95, with a maximum at DAP 49 when flowers were sampled for the first time. In the neighborhood of the cowpea fields, a diverse population of alternative host plants was monitored weeks before flower set in cowpea (Fig. 7.8.); considerable numbers of thrips, particu-

larly larvae, were observed. Their sudden migration into the cowpea fields right at the start of flowering might have led to shedding of flowers, which did not favor a population build-up of thrips in these fields.

In parallel to the steady decline in flower numbers in the cowpea, larval numbers decreased and adults' numbers dropped markedly possibly indicating a migration away from cowpea in search of more favorable feeding and ovipositing sites. Seasons I/96 and II/96 peaked in favor of fertilized plots. In the early flowering (DAPs 35, 42) in both seasons the amount of rainfall enabled the fast dissolution of the applied nutrients. In season I/96 rains continued at very low levels during the flowering peak, and they completely ceased in season II/96. The lack of rainfall kept nutrient leaching at a low level, but did not trigger drought stress. This assured a permanent nutrient flow in favor of the nitrogen-dependent (fertilized) plants (Wien & Summerfield 1984). After DAP 63 the fertilized plants in season I/96 started flowering anew with increasing rainfall at this time and the probably still remaining nutrients due to low leaching (Fig. 2.12.). In season I/97 the larval population of thrips built up early at DAP 42 due to high levels of adults, which probably migrated into the cowpea from neighboring alternative hosts, particularly *Tephrosia bracteolata*, that had carried a moderate population of thrips weeks before the flowering of the cowpea. Both stages, adults and larvae, showed preferences for the fertilized plots, which apparently led to the drop in flower numbers in the fertilized plots. Peaks of thrips abundance in non-fertilized plots occurred one week later and were probably less detrimental to flower set. At DAP 56 rainfall increased again, enhancing vegetative growth in fertilized plots (Fig. 2.14.) and further suppressing reproductive development.

Flower index. Season I/95 did not result in differences since better developed plants also yielded more flowers. Seasons II/95-I/97 revealed a more favorable index for non-fertilized plots. Plants were always much smaller without fertilizer and recorded in season II/95 slightly and in season I/97 significantly more flowers without fertilizer, producing a higher ratio. For season I/96 fertilized plants at DAP 63 were about four times bigger than those without NPK. Although more flowers were recorded under fertilizer as well, this difference was much less than fourfold, which explains the higher index without fertilizer. The index in season II/96 was slightly higher at DAP 49 for fertilized plots due to the higher flowering peak in these treatments. One week later this difference in flower numbers became obsolete while fertilized plants still grew. Thus, the index turned in favor of non-fertilized plots. A positive index in season I/97 for the control can be explained by comparatively smaller plants and in turn slightly more flowers in contrast to the index for both mulch types.

Pods. Straightforward from flower patterns in season I/95, pods did not show differences. Whereas non-fertilized plots produced very low pod numbers, having produced about the same flower quantities, fertilized pods recorded marginally more pods per plant. NPK might have increased plant vigor, resulting in higher pod set. Towards DAP 56, when rainfall peaked, plant growth increased visibly (Fig. 2.11.). Fertilizer probably became better available

due to this peak. A switch back to vegetative development in these treatments may have increased shedding of premature pods since fertile soils favor vegetative growth (Sellshop 1962). Non-fertilized plants remained very small, probably because of overall limited precipitation. Permanent high and even rising thrips pressure in the neighboring alternative hosts, particularly *T. bracteolata, Tephrosia platycarpa,* and *Cochlospermum planchoni* (Fig. 7.8.), were possibly the origin of high flower shedding resulting in low pod output in all treatments.

Seasons I/96 and II/96 yielded more pods from fertilized treatments, the effect of which was much stronger in season II/96. Although flowers peaked higher in fertilized treatments during season I/96, the output in pods was only marginally better than non-fertilized plants. Adult thrips had a peak one week before flower maximum (DAP 42) in the same plots, possibly reducing flowers considerably. Since larval abundance strongly increased after the flower peak, in particular for fertilized treatments, the higher flower numbers in these plots supposedly suffered more shedding. After DAP 63 flower numbers in fertilized plots rose again with increasing precipitation. Since the thrips population had already collapsed at this time, flowers developed directly into pods. As for season II/96, higher flower numbers in fertilized plots straightforward became pods (Fig. 2.13.). The sudden increase in pod numbers between DAPs 42 and 49 happened when larval abundance was still very low and adults were about to increase densities but had not caused high damage yet. This sudden increase in pod numbers at the beginning and the subsequent moderate growth confirms the findings of Ojehomon (1968) and Summerfield & Roberts (1983) that early flowers are most likely to produce fruits while flowers of the second half of anthesis contribute much less to yield. Flower production in season I/97 led directly to the same patterns in pod set with a more favorable output in non-fertilized plots. Whereas increasing precipitation led to a switchback into vegetative growth in fertilized plants on the basis of applied nutrients, the nodulated, non-fertilized plants used the higher water availability for reproductive growth and only moderately reacted with increased vegetative mass. The control produced more pods than both mulch types despite recording the smallest plants. Slightly more flowers were counted in the control and the peaks in larval thrips numbers were more elevated at DAP 49 in mulch plots. Higher flower shedding in mulch plots might have caused this reduced pod set.

IITA

Nodes. The differences in season I/95 between the control and neem, as well as *Senna* with *Imperata,* both having developed bigger plants may be explained by slightly higher values for phosphate in the upper soil layer, carbon in both strata and nitrogen in the upper layer. The slightly higher nitrogen and phosphate levels may have stimulated nodulation (Tewari 1965; Summerfield et al. 1974; Eaglesham et al. 1977). Except for the neem plots, the mulches increased plant growth, which is confirmed by Masefield (1957) and Terada (1971) referring to enhanced nodule production by applied organic matter. Neem produced at least marginally

bigger plants than the control (Fig. 2.15.). Neem possibly was inferior to *Senna* and *Imperata* mulch due to a slightly lower concentration of phosphate in the upper stratum, carbon and nitrogen in both layers, potassium in the upper, and magnesium in the lower stratum. No significant treatment differences were suggested in season II/95 but plants under neem developed visibly better than those under *Senna* (Fig. 2.16.), recording slightly higher values for cation exchange capacity in both layers and phosphate and carbon in the upper soil stratum.

Although in season I/96 plants under *Imperata* mulch were larger than those under *Senna* (Fig. 2.17.), this variation was very narrow. Because there was no evidence of supporting patterns in the soil, no attempt has been made to explain these findings further. Variation in season II/96 was not significant and existing tendencies (Fig. 2.18.) could be explained with corresponding patterns in the soil. Distinct differences prevailed during season I/97 when the control recorded significantly smaller plants than the three mulch types (Fig. 2.19.). No clear patterns were found in the soil samples, indicating no soilborne influence. Rather, the underlying results confirm findings on increased vegetative development due to improved soil humidity, higher nodule numbers and nitrogenase activity, more efficient water use, and increased pore volume, hydraulic conductivity, and earthworm and microbial activity as well as cation exchange capacity following mulch application (Masefield 1957; Terada 1971; Kamara 1980; Schoningh 1985; Remison & Mgbeze 1987; Daisley et al. 1988; Yih & Vandermeer 1988; Gupta & Rao 1989; Salau et al. 1992; Owino et al. 1993; Adetunji 1994).

External influence by thrips can be excluded, although it would have supported these findings since the indeed higher abundance in all mulch treatments (Fig. 3.15.) might have increased flower shedding leading to abnormal plant growth (Lawrie & Wheeler 1974). The observed difference in treatments occurred right at the beginning of physiological observations, hardly increasing in trend. Thrips numbers at the same time (DAP 42) were still close to zero and peaked late (DAP 63), without any supposed influence in the way described above. Plants in seasons I/95-I/96 ceased their vegetative development after DAP 56; they were smaller in seasons II/96 and I/97 and nearly stopped growing after DAP 49. Plants in season II/96 suffered obvious drought stress, which results in reduced shoot dry matter (Turk & Hall 1980b; Wien & Summerfield 1984) caused by limited nodulation (Summerfield et al. 1974). Although precipitation was relatively high during season I/97 and no nutritional patterns in the soil were recorded, the vegetative mass overall was very low. The pH values in both strata were the lowest measured throughout five seasons in all three regions (<4.7). These extremes possibly fixed vital micronutrients like molybdenum (Sellshop 1962), which were not covered by the analysis.

Flowers. Although no significant multivariate differences were found throughout seasons I/95-II/96, seasons I/95-I/96 visibly offered some marginal variation. *Imperata* treatments peaked highest during season I/95, responding to slightly higher phosphate concentrations in the soil. Season II/95 yielded low flower numbers and the variation among treatments was regarded as noise where no soilborne or external patterns (e.g., thrips damage) could be fitted.

Univariate analysis in season I/96 uncovered a significant difference between neem and the control that could not be explained by soilborne patterns. During this season comparatively high numbers of larvae of *M. vitrata* were found (Fig. 3.13.), probably explaining these patterns. Neem revealed highest flower peaks but lowest numbers of *M. vitrata*, which were most abundant in the control; this probably led to higher flower shedding through damage to inner floral tissue. Thrips damage leading to this variation can be excluded since their population at DAP 49 was below 10 larvae and adults per flower. The variation in flowers followed the patterns, which were observed for vegetative growth. Mulch favored flowering in the same way as it strengthened plant growth as described above. Although in season I/97 the control showed significant variation from neem and *Imperata* only, a tendency for all mulch treatments contrasting the control is visible (Fig. 2.19.). *Imperata* with its higher lignin contents probably kept soil humidity longer, followed by the faster decomposing mulches – neem and *Senna* (Stigter et al. 1994) – despite no significant differences in the soil samples.

Flower index. *Imperata* produced most flowers in season I/95 but developed the biggest plants together with *Senna*. The low index in season II/95 came about by low flower numbers on big plants. Season II/96 recorded a slightly higher index for *Senna* on the basis of marginally more flowers on better developed plants. A distinctively higher index for neem treatments in season I/96 was produced as comparatively smaller plants counted by far the most flowers compared with all other treatments (Fig. 2.17.). Although no clear trend was revealed in season I/97, plants in *Imperata* counted more flowers but were second smallest.

Pods. The control as well as *Senna* and neem mulch did not vary in flower numbers during season I/95 but both mulch treatments showed a slightly higher pod set than the control, which can be ascribed to the more favorable condition mulch provides to the plant (Masefield 1957; Terada 1971; Schoningh 1985; Daisley et al. 1988; Yih & Vandermeer 1988; Gupta & Rao 1989). Plants under *Imperata* mulch responded much more strongly in flower numbers but could not maintain them for pod set, since higher numbers bear the risk of higher losses through natural shedding (Ojehomon 1968). Adult thrips steadily rose in numbers in *Imperata* mulch, possibly exerting an additional effect through damage. Pod setting in season II/95 was the direct result of flower numbers, which turned into pods according to their respective levels. Although higher flower numbers were counted in all mulch treatments, the most pods were obtained in the control. This difference in terms of existing pods at the moment of peak flowering does not suggest these differences at the origin of the particular pod set. Soilborne influences could not be found to support this either. Pest influence was excluded since thrips populations rose towards DAP 56 to their highest numbers and *M. vitrata* right at DAP 49 had its first considerable increase, both appearing too late. If they had been on time, both pests would have suggested exactly the opposite since the control was attacked most.

In season II/96 plants developed most nodes and produced slightly more flowers, which led to highest pod set based on the most favorable phosphate levels in the soil. The beneficial effects of this nutrient on nodulation and subsequent plant development (Tewari 1965; Rachie

& Roberts 1974; Summerfield et al. 1974; Munns 1977 cited in Wien & Summerfield 1984; Cadisch et al. 1989) resulted in these responses. *Imperata* plots recorded in turn the lowest phosphate levels, which were at least partly responsible for low pod set. Although plants under *Imperata* mulch counted most flowers after DAP 56, and the respective increase in pod numbers was visible (Fig. 2.18.), this flowering effect was minor since late flowers contribute only little to yield (Ojehomon 1968; Summerfield & Roberts 1983). During season I/97 flower numbers turned directly into the same patterns of pod set (Fig. 2.19.); *Imperata* was highest and neem second highest, undisturbed by thrips attacks, which appeared late (Fig. 3.15.), and under well-watered conditions (Table 2.6.). The early flower peak (DAP 49) could fully turn into fruits in this phase, making a strong contribution to economic yield (Rachie & Roberts 1974; Summerfield & Roberts 1983; Summerfield et al. 1983).

Conclusions

This study assessed the effect of two factors, NPK fertilizer and different mulch types, on cowpea development in terms of vegetative and reproductive growth. Other measured effects were also sought to explain basic environmental influences like soil quality, climate, and attacks by herbivores. Mulch, which was the crucial point of concern of this study, turned out to produce only marginal impact on plants. In turn, nutritional effects, pest abundance closely related with its timing, and weather conditions dominated plants' development. The various beneficial effects of mulch are commonly recognized. The longer the time of decomposition, the greater these effects will be. In the present study a cowpea variety was used that was harvested not later than 77 days after planting (DAP). The benefits of mulch due to ongoing decomposition at harvest thus should not be overestimated. Since mulch was applied on all seasonally shifted fields for the first time, the known temporary fixation of nitrogen (Müller-Sämann & Kotschi 1997) may hinder several of the positive effects. Supposed physical effects on water resources or soil temperature obviously were not met or were masked by interacting factors, e.g., pests.

Fertilizer application and pest influence were dominant influences on plant development. NPK application generally boosted vegetative growth, often positively influencing flower set. Thrips had a markedly detrimental consequence for flower numbers whenever their peak abundance coincided with the plant's early reproductive growth. This was of major impact on reproductive growth both among seasons across years and across regions. In addition, thrips' abundance was found to interact with fertilizer.

None of the cited factors can be treated individually. The results identified several two-level interactions, consisting of a direct and an indirect relationship. Three direct interactions were separated between 1) fertilizer and soil, 2) soil and plant, and 3) plant and thrips. The indirect relationships consisted of 1) soil via plant and 2) fertilizer via soil and plant, which

both influenced thrips. This interaction complex made it difficult to obtain any overall main effect, the NPK influence as well as the thrips damage being the most evident factors.

Three recommendations are to be drawn from the underlying study. It obviously does not make sense to use NPK fertilizer on this leguminous plant. Less poor soils (Tokpa/Ayou) may lead to very good yields without fertilizer, given a limited pressure of external influences. The low direct effect of fertilizer does not justify the high input costs. On comparatively poor soils (Lema), the application of nutrients (NPK) principally forced unnecessary vegetative overgrowth to the disadvantage of the reproductive phase. Thrips' preference for well-nourished plant tissue might worsen this outcome, additionally causing increased flower shedding. If fertilizer can be afforded, the application to a preceding crop is to be suggested. Pest attacks, particularly by thrips, are known to reduce flower numbers considerably as well as economic yields if they coincide with early reproductive growth. This was confirmed several times throughout this study.

Effective pest control ranks highest among all possible improvement efforts to considerably increase yields. The study has shown that losses on reproductive organs due to thrips are distinct during late cropping seasons. As practiced by many farmers in the coastal areas of Benin, cowpea cultivation is not to be encouraged in late growing seasons if effective protection cannot be assured. Very early planting dates, in turn, revealed high yields without any attempt to protect against pests.

Although mulch did not reveal great impact on plant growth during this study, this does not negate its use as a high potential means of improving soil conditions. The short growing cycle of the cowpea variety under study did not fully make use of the ongoing decomposition of the organic material. It is believed that the long-term use of mulch for cowpea cultivation might considerably improve the growing conditions while better exploiting the undoubtedly very high yield potential of this plant.

3 Population dynamics of *Maruca vitrata* F. (Lepidoptera: Pyralidae) and *Megalurothrips sjostedti* Trybom (Thysanoptera: Thripidae) in flowers of cowpea as influenced by applied mulch on two different levels of chemical fertilizer NPK

ABSTRACT Efforts to use organic soil cover as protection against pests in cultivated crops have so far not revealed conclusive effects. Rather, results range from negative to positive impact on pest abundance. As an attempt to explain the abundance of *Maruca vitrata* F. (Lepidoptera: Pyralidae) and *Megalurothrips sjostedti* Trybom (Thysanoptera: Thripidae), this study combined three different mulch types with applications of chemical fertilizer (NPK). To adjust for several known external influences, plant physiology, soil properties, climatic conditions (precipitation, temperature), and the composition and carrying capacity of alternative host plants in the vicinity of the cowpea fields were taken into consideration. Three different regions were chosen assuming different climatic conditions and abundance of wild host plants. Mulch was found to increase flower numbers of cowpea in those cases where its influence could be isolated, thus accounting for indirect influences on pests. In one case only a shelter effect was assumed, which was linked to particularly dry conditions. Flower numbers generally responded positively to NPK application and suggested a favorable change of plant metabolism that met the needs of developing larvae more efficiently and also increased plants' suitability for adults' oviposition. External factors like climate and alternative host plants were considered dominant over plot inherent conditions to a limited extent for *M. vitrata* but considerably for *M. sjostedti*. Additionally, the population development of *M. vitrata* appeared to depend on thrips densities and time of migration into cowpea flowers. Given low precipitation, thrips appeared during early flower set, with the resulting damage and flower shedding preventing *M. vitrata* from establishing important populations. High overall precipitation during the cropping season or peak rainfall coinciding with flower peaks obviously reduced or delayed migration by *M. sjostedti*. These were situations, where higher flower numbers were counted and *M. vitrata* built up larger populations. Delayed thrips migration generally led to moderate or low oviposition in cowpea due to decreasing suitability of aging plants. Mulch effects on pests in general appeared weak, and whether considered alone or in combination with NPK, tended to increase pest populations. NPK positively influenced flower numbers as well as pests' population build-up. In view of the increasing effect on pest populations, direct NPK application to cowpea was not recommended, and high labour input for mulch allocation under these short-term conditions could not be justified. Furthermore, accumulation of thrips numbers towards later cropping seasons in cultivated and wild hosts suggested early cowpea cultivation. Where late cowpea cannot be protected efficiently, yield potential is drastically reduced below economically meaningful levels.

The agronomic importance of mulch is unquestionable (Masefield 1957; Terada 1971; Rachie & Roberts 1974; Kamara 1980; Schoningh 1985; Remison & Mgbeze 1987; Daisley et al.

1988; Yih & Vandermeer 1988; Gupta & Rao 1989; Salau et al. 1992; Owino et al. 1993; Adetunji 1994; Müller-Sämann & Kotschi 1997), whereas its use to influence pest populations is still a matter of some controversy. Effects of mulch range from suppression of insect populations due to disturbance of visual stimuli, odor, plant camouflage, increased activity by predators, and reduced moisture stress (Arthur 1962; Ackland 1971, cited in van Rijn 1982; Allison 1973; Litsinger & Ruhendi 1982; Ruhendi et al. 1982), over no effects (Violic et al. 1982), up to an increase of insects by providing shelter, increased soil humidity, or other conditions for better development due to undisturbed soil surface in no-tillage systems (Le Pelley 1968 and Lee & Wood 1971, cited in Türke 1976). This might have important implications for *M. vitrata* and *M. sjostedti*, both of which are known to pupate in the soil litter (Taylor 1967; Rösingh 1980; Mollema & Cole 1996). At this susceptible stage mortality ascribed to predators, fungi, or perhaps breeding parasitoids may have consequences for the consecutive population build-up. Mulch can also improve the effect of applied chemical fertilizer (Wade & Sanchez 1983), while increasing humidity under dry conditions or reducing leaching due to high precipitation (Reijntnes et al. 1992; Hagmann & Murwira 1996; Hiol Hiol et al. 1996; Mangisoni & Phiri 1996; Slingerland & Masdewel 1996; Müller-Sämann & Kotschi 1997). Consequently, changing metabolism in plants is likely to bias pests' searching behavior for optimum nutrition uptake (Painter 1951; Fennah 1963; Lewis 1973; Southwood 1973; Scriber 1984; Ananthakrishnan & Gopichandran 1993; Bentz et al. 1996; Mollema & Cole 1996). Larval survival, female fecundity (White 1984), and adults' longevity, which was increased through nitrogen application for *S. calamistis* by Sétamou et al. (1993, 1995), may also play an important role.

There is evidence that insects' digestive systems are stimulated and influenced by the amount of protein and the composition of amino acids inherent in the food source. As they feed on the plant, insects' digestive enzymes are released and, depending on additional external supply of amino acids or enzymes, the digestion is catalyzed (Baker 1977; Lehane 1977; Walker et al. 1980; Chapman 1985).

However, the cowpea field is not a closed system and is subject to strong external influences, e.g., alternative host plants (Wolda 1988; Tamò 1991; Ananthakrishnan & Gopichandran 1993; Leumann 1994; Arodokoun 1996). Both pests do not diapause, but shift between the overlapping flower cycles of a wide range of alternative host plants, which are found in fallows and wild habitat. Although reduced in numbers (Taylor, 1967) during dry seasons, their short generation interval enables these pests to respond rapidly to any increase in suitable feeding sites. High migration leads to inundation of neighboring cultivated areas, e.g., cowpea fields, and can cause tremendous losses to reproductive organs (Taylor 1964; Singh & van Emden 1979; Wien & Tayo 1979; Atachi & Ahohuendo 1989; Singh 1990; van de Klashorst & Tamò 1995). Since overall monitoring of regionally occurring host plants is generally not feasible, neighboring strips of land were screened regularly for estimates of pest population status around the cowpea fields. Cases occurred where considerable migration had

to be assumed despite negligible population size in few alternative hosts. *M. sjostedti* is easily carried by wind (Lewis 1973) and even larvae of *M. vitrata* were reported to be transported by wind. Bottenberg (pers. comm.) found larvae on sticky traps set at a height of 70 meters, which probably explains these particular cases.

Materials and Methods

Insect counts in flowers. For studies on population dynamics of both pests over time, shoot tips, flower buds, and flowers (according to the growth stage of the crop) were collected randomly in weekly intervals. Since these organs are considered the main sources of development (Ghesquière 1942; Taylor 1967, 1969, 1978; Woolley & Evans 1979; Tayo 1988; Firempong & Magalit 1990; Tamò et al. 1993b) (*M. vitrata* generally builds up its population on flowers and completes its life cycle on pods), the method is valid for *M. vitrata* and *M. sjostedti* as well (Atachi & Ahohuendo 1989). Each of the 20 plants per plot was selected using a table of random numbers representing a combination of line number with plant number within lines. The amount of 20 flowers was considered to be a realistic sample size for statistical analyses as well as handling for dissection (Atachi & Ahohuendo 1989; Ofuya 1989; Tamò et al. 1993b). One organ was taken per plant and pinched into a plastic vial (3.5 x 8 cm; 6 x 6.3 cm; 6 x 10 cm – diameter x height for three different sizes) containing 50% alcohol (local distillate) (Salifu & Singh 1987). To minimize the number of thrips taking off during the exercise, sampling took place in the early hours of the morning (7:00-10:00) before the peak flight activity (Taylor 1969). Flower sampling in alcohol was always the very first step each sampling day to approach a completely untouched field with minimum losses of thrips flying off after disturbance. Nobody was supposed to enter the field for two days before sampling (e.g., for weeding) to assure a more or less stable population the day of flower collection. The sampling methodology used by Atachi & Ahohuendo (1989), i.e., to collect one organ per vial, was considered too labor intensive and could not be applied. Instead, 20 flowers were collected in one vial per treatment (shoot tips and flower buds, respectively) and for each sampling date (Sétamou et al. 1995; Vanleeuwen et al. 1996). Since insect distribution implies a considerable variation that might cancel out possible treatment disparities, the use of mean scores per plot was expected to show differences, if present, more clearly (Korie, pers. comm.).

Sampling of organs was started usually at DAP 35 and suspended the day of harvest in the first three seasons (I/95, II/95, I/96) to be sampled. In later seasons this was prolonged to tentatively include the point where the drop in population would indicate the migration away from cowpea (Tamò et al. 1993a) to other feeding sites. The organs were dissected in the laboratory and thrips (following Palmer 1990), the pod borer (following Taylor 1967), and antagonists were identified and counted under the binocular. Larvae and adults of *M. sjostedti* were separated through counts for further individual analyses. Since their distinct feeding behavior (Tamò et al. 1993b) has clear-cut consequences for the plant, their respective abundance levels

have to be interpreted in a different light. An attempt to consider separately early instars (first-third instar) and late instars (fourth, fifth) of *M. vitrata* failed because the generally low abundance often did not reveal a certain number of larvae per instar group for proper analyses. Means to be used for graphs are reported per 20 flowers for *M. vitrata* whereas *M. sjostedti* was referred to on a per-flower basis.

Density index. Insect counts per unit (mean score of 20 randomly selected flowers), which are further called abundance, are strongly influenced by the surrounding availability of resources. Differences between counts may simply occur due to variation in flower abundance in the respective sampling area (e.g., treatments). To overcome this bias, an index was created that considers relative insect density per actual number of flowers:

$$\text{Density (index)} = \frac{\text{number of insects per flower (abundance)}}{\text{mean number of flowers per 10 plants}}$$

This index adjusted for actual flower numbers in the respective treatments. To use this quotient, the real abundance was calculated given that all treatments would have produced the same number of flowers. For each sampling day counts for phenology revealed the perceptible number of flowers (mean per 10 randomly chosen plants) in each treatment. Insect counts were accompanied by this index to detect "false differences", which would have occurred when not considering the actual number of flowers.

Statistical analysis. Equally spaced sampling dates allowed application of repeated measures analysis (ANOVAR) (Greenhouse & Geisser 1959; Huynh & Feldt 1970; Hand & Taylor 1987; Potvin et al. 1990; Vanleeuwen et al. 1996). Mean scores of 20 flowers per plot were used as responses. ANOVAR for mixed models was carried out, using polynomial trend contrasts for profile analyses. *F*-values were marked with $^{[l]}$,$^{[q]}$, or $^{[c]}$ if tested on the linear (first order polynomial), quadratic (second order polynomial), or cubic trend (third order polynomial), respectively. Data were $\sqrt{(x + {}^{3}/_{8})}$ transformed if necessary (after investigation of standardized residuals). The density index, being a ratio, was arcsine $\sqrt{p}$ transformed before analysis.

After each ANOVAR, least squares means served as tool for separation of means. To account for *a priori* chosen treatment differences, orthogonal contrasts were selected. Since contrasts can represent combinations of comparisons as "weighted sum of means" (Hand & Taylor 1987, p. 10), they were used to compare different clusters, e.g., first growing seasons (I/95, I/96, I/97) against second growing seasons (II/95, II/96), or no mulch (control) versus mulch ([*Senna siamea* (called *Senna*) + *Imperata cylindrica* (called *Imperata*)]/2).

To distinguish seasonal and regional patterns, a factorial ANOVA across time was preferred over repeated measures. The distinctly different profiles within each season and between first and second rainy seasons did not allow proper comparisons of trends. Instead, seasons and regions were incorporated as additional factors. For comparisons between regions and between

seasons within regions, replications were nested within region and season, respectively, to use a hierarchical error term (Korie, pers. comm.).

A *P*-value of 0.05 was generally used to judge significance, although higher levels were considered as marginal responses if reckoned important. *F*-values were marked with one star (*) if $0.05 > P \geq 0.01$ and with two stars (**) if $P < 0.01$.

The exact description of experimental sites and the research design, auxiliary data like climate and soil properties, and a detailed description of the statistical approach were discussed completely in Chapter 1 and may assist in further understanding.

Results

Regional differences

NPK was not used at IITA. Hence, regional differences were tested in two steps. An overall comparison of the three regions did not consider NPK, leaving mulch as the single treatment factor. The neem treatment at IITA was excluded as well, which was a special component for the on-station trials only. A second step compared the two on-farm regions Tokpa/Ayou and Lema, controlling for NPK.

All regions

Maruca vitrata. In all five seasons the pod borer was three times more abundant in Lema (1.7^{d} larvae per 20 flowers) compared with IITA (0.6^{d}) ($F = 34.4^{**}$) (Table 3.1.). For II/95, I/96, II/96, and I/97 Lema also attracted more *M. vitrata* than Tokpa/Ayou. In I/97, numbers were lower at IITA than in Tokpa/Ayou. ($F = 2.7^{*}$). The density index for *M. vitrata* was three times higher in Lema than at IITA and twice that of Tokpa/Ayou across all seasons ($F = 30.2^{**}$).

Megalurothrips sjostedti. Larvae and adults of the flower thrips did not vary greatly in abundance between regions and seasons (Table 3.2.). On a seasonal basis, larvae and adults showed the same abundance patterns between regions except during II/96 when larval numbers were not different between regions but adults were by far fewer at IITA (5.2^{d}) than in either Tokpa/Ayou (22.8^{d}) or Lema (25.3^{d}). The density index for adults was at the same time higher in Lema during II/96 in contrast to Tokpa/Ayou and IITA, the latter yielding the lowest index ($F = 11.9^{**}$) (Table 3.3.). Considering the remaining seasons, Lema had lowest larval numbers (5.2^{d}) in I/95, contrasting with Tokpa/Ayou (12.2^{d}) and IITA (15.8^{d}), but larval abundance in Lema (13.2^{d}) was highest in I/97 compared with Tokpa/Ayou (8.6^{d}) and IITA (5.5^{d}). In II/95 IITA (24.8^{d}) attracted highest numbers of larvae and was superior to Tokpa/Ayou (14.4^{d}) and Lema (5.9^{d}). During I/96 fewer larvae were counted per flower in Tokpa/Ayou (4.0^{d}) than

IITA (10.2^{d}) and Lema (11.9^{d}) ($F = 10.8^{**}$). The patterns for adults behaved in the same way, with the *F*-values differing slightly. Except for season II/96, the density index did not differ among regions in the other seasons.

On-farm regions

Maruca vitrata. In addition to the regional variation the pod borer was more abundant in fertilized plots (1.5^{d} larvae per 20 flowers) in comparison to blank ones (1.2^{d}) ($F = 6.1^{*}$). Densities did not respond to NPK application in either region.

Megalurothrips sjostedti. When considering thrips without distinction between larvae and adults, a marginal, non-significant effect of NPK was noticed. That is, 11.3^{d} thrips were sampled per flower on average in fertilized treatments, while the non-fertilized plots had a mean of 10.2^{d} ($P \geq 0.05$). No fertilizer impact on preference was found when analyzing larvae and adults separately. Densities did not change due to application of fertilizer for either stage of thrips.

Seasonal differences within the same region

Tokpa/Ayou

Maruca vitrata. *M. vitrata* occurred in highest numbers during season I/95 (Table 3.4.). While season I/95 (1.8^{d} larvae per 20 flowers) did not differ from I/97 (1.4^{d}), it did reveal a significantly higher abundance than seasons II/95 (0.4^{d}), I/96 (1.0^{d}), and II/96 (0.3^{d}) ($F = 12.2^{**}$). Season II/96 had the lowest counts and was significantly less than seasons I/95, I/96, and I/97. The first growing seasons (I/95, I/96, I/97) yielded higher counts than second seasons (II/95, II/96). These patterns of abundance were recorded together with a density index, which did not vary among seasons.

Megalurothrips sjostedti. Thrips were more abundant in second rainy seasons (II/95, II/96) compared with all first seasons (I/95, I/96, I/97) ($F = 21.9^{**}$). This was also true separately for larvae and adults. The two thrips stages together were denser in the second growing seasons compared with the first seasons (Table 3.6.). The same applied for larvae and adults separately. A comparison of seasons in particular showed that the variations in larval numbers among seasons were different from those of adults (Table 3.5.). As for larvae, season I/96 displayed remarkably lowest abundance with 4.0^{d} larvae per flower – far below seasons II/95 (14.4^{d}), II/96 (12.5^{d}), I/95 (12.2^{d}), and I/97 (8.6^{d}) ($F = 11.2^{**}$). The larval density index was lowest in season I/96 and differed significantly from seasons II/96 and II/95 ($F = 4.5^{*}$). Season II/95 had the highest abundance but differed significantly from seasons I/96 and I/97 only. Adults showed highest abundance during season II/96 counting 22.8^{d} adults per flower (*F* =

15.3**) (Table 3.5.). All other seasons had significantly lower means; in decreasing order these were seasons II/95 (14.8^{d}), I/95 (11.5^{d}), I/97 (7.9^{d}), and I/96 (5.6^{d}). Season I/96 yielded the lowest adult numbers, from which seasons I/95, II/95, and II/96 deviated in increasing quantities. Adults recorded highest densities in II/96, whereas I/96 had a significantly lower index than II/95 and II/96 ($F = 9.3^{**}$).

Lema

Maruca vitrata. Generally more larvae of *M. vitrata* were counted in fertilized treatments than in plots without NPK (2.0^{d} with/1.5^{d} without NPK) ($F = 6.9^{**}$). However, when focusing on fertilized treatments only (simple effects), abundance was highest in season I/96 with a mean of 2.9^{d} in 20 flowers compared with seasons II/95 (1.3^{d}) and I/97 (1.5^{d}) ($P \geq 0.05$). These results were of marginal importance after ANOVA and not significant, although the use of contrasts suggested these differences. The densities as expressed by the index did not reveal a response to treatments.

Megalurothrips sjostedti. A significantly different abundance among seasons was found between larvae and adults ($F = 8.1^{**}$). Larvae were found in higher numbers in both first rainy seasons I/96 (11.9^{d} larvae per flower) and I/97 (13.2^{d}), compared with seasons I/95 (5.2^{d}) and II/95 (6.0^{d}), which remained close together at a significantly lower level ($F = 3.6^{*}$) (Table 3.7.). The highest index for larvae appeared during season II/96, which was significantly more than for seasons I/95, II/95, and I/96 ($F = 4.0^{*}$). While season I/97 did not record differences from II/96, this was still higher than seasons II/95 and I/96 (Fig. 3.8.). Adults in turn showed highest abundance during season II/96, with a mean of 25.3^{d} that was significantly different from seasons I/97 (13.1^{d}), II/95 (10.4^{d}), and I/95 (2.8^{d}) ($F = 10.2^{**}$). Significantly lowest adult numbers were counted in season I/95. Season I/96 (16.5^{d}) was not different from II/96. Adults in season II/96 showed the highest density index among seasons. Season I/97 was also higher than season I/95 ($F = 13.0^{**}$).

IITA

Maruca vitrata. Larval abundance in seasons I/95 (1.1^{d} larvae per 20 flowers) and I/96 (1.1^{d}) was significantly higher than in seasons II/95 (0.1^{d}) and II/96 (0.1^{d}) ($F = 5.5^{*}$), the two pairs not differing within each other. The variation between all first cropping seasons deviated significantly from the one inherent in second seasons per year, the number of the latter being remarkably low. Differences in the density index were marginal after ANOVA ($P \geq 0.05$). Contrasts revealed that season I/96 showed higher densities than season II/96, which accompanied the same findings on larval abundance.

Megalurothrips sjostedti. Larval abundance did not differ markedly from adults' over seasons. Larvae appeared in higher numbers in season II/95 (25.8^{d}), which was significantly

different from seasons I/96 (10.0[d]), II/96 (9.7[d]), and I/97 (5.4[d]), all being close together (F = 11.9[**]) (Table 3.9.). Season I/95 (16.4[d]) also revealed higher numbers than season I/97. As for adults, seasons II/96 (5.3[d]) and I/97 (4.7[d]) showed no differences but were considerably lower than seasons I/95 (17.2[d]), II/95 (24.6[d]), and I/96 (11.2[d]) (F = 18.5[**]). Within the latter cluster season II/95 scored significantly higher than I/96. The density index for adults was also higher in season II/95 than in I/96 (F = 4.5[*]) (Table 3.10.).

Differences within seasons

Although the figures generally consist of letters a)-d), and a)-f) for several cases, a) is not mentioned in the text. This part displays data on precipitation and temperature and serves as complement for the subsequent components of the figures.

Tokpa/Ayou

First season (I/95)

Maruca vitrata. A marginal trend difference was found for the NPK effect over time on the second order polynomial ($P \geq 0.05$) (Fig. 3.1b.). In plots with applied NPK, the population of *M. vitrata* peaked higher at DAP 56 with 5.5[d] larvae per 20 flowers than blank plots (4.0[d]) but decreased faster afterwards. The densities remained similar among treatments (Fig. 3.1b.).

Megalurothrips sjostedti. Thrips in total revealed an inverse mulch effect due to fertilizer application (F = 3.3[*]). Under no NPK application, the control (23.0[d]) showed higher abundance than *Senna* (20.6[d]). In the plots where fertilizer was used, the control (17.6[d]) had lowest thrips numbers and *Senna* was highest (23.5[d]). Differences between larvae and adults were not significant. Larvae separately showed different profiles on NPK levels over time (F = 2.9[[q]*]) (Fig. 3.1c.). Larval numbers grew slightly faster in fertilized plots to a peak (51.2[d]) at DAP 63, but dropped in numbers, while the population in plots without NPK still grew to 57.0[d] larvae per flower at DAP 70. Adults were not influenced by any treatment (Fig. 3.1d.). Their peak (56.3[d] with and 50.1[d] without NPK) was also at DAP 63. Larval and adult densities were similar (Fig. 3.1c,d.). The index reached its maximum at DAP 63.

Second season (II/95)

Maruca vitrata. None of the treatments influenced larval numbers (Fig. 3.2b.).

Megalurothrips sjostedti. Larvae and adults did not demonstrate treatment effects (Fig. 3.2c,d.), but their respective dynamics over time were significantly distinct from each other (F = 23.1[**]). Larvae remained at a much lower level than adults and rose to their maximum (33.9[d] with and 43.4[d] without NPK) at DAP 70. For the fertilized plots, a short setback occurred at

DAP 63. Abundance in fertilized treatments was slightly higher. Adults sharply peaked at DAP 63 (77.6^{d} with and 72.6^{d} without NPK) and the population collapsed steeply the week after. The corresponding densities did not show significant variation.

Third season (I/96)

Maruca vitrata. *M. vitrata* did not react on different treatment conditions and peaked at DAP 56 (5.5^{d} larvae per 20 flowers with and 4.1^{d} without NPK) (Fig. 3.3b.).

Megalurothrips sjostedti. A significant difference in population dynamics between larvae and adults existed over time ($F = 35.6^{**}$) (Fig. 3.3c,d.). Larvae responded marginally to treatments on the trend ($P \geq 0.05$) (Fig. 3.3c.). The profile for NPK^{+} plots increased faster and fell short of the level for non-fertilized plots, which peaked higher (29.7^{d} larvae per flower) at DAP 63 (24.5^{d} with NPK). Adults showed higher abundance across time in the fertilized treatments ($F = 7.0^{*}$) (Fig. 3.3d.). The peak at DAP 70 was higher in fertilized plots (25.9^{d}) than in NPK^{-} treatments (20.5^{d}).

Fourth season (II/96)

Maruca vitrata. In combination with NPK fertilizer, *M. vitrata* was influenced inversely by mulch. Without NPK *Imperata* mulch yielded most larvae (1.6^{d} larvae per 20 flowers), whereas fertilizer effects lowered the population in *Imperata* considerably (0.3^{d}) ($F = 4.8^{*}$). The contrary happened for the control (0.4^{d} without NPK), which demonstrated a slight increase through fertilizer application (0.7^{d}). *Senna* mulch remained at the lowest level and dropped in larval numbers from 0.3^{d} (without NPK) to 0.1^{d} due to fertilizer application. Profiles for the NPK effect over time suggested a marginally lower peak for non-fertilized plots (0.7^{d}) at DAP 63 than for the ones with NPK (1.9^{d}) ($P \geq 0.05$) (Fig. 3.4.).

Megalurothrips sjostedti. Larvae and adults developed differently over time ($F = 122.1^{**}$). Larvae themselves did not react on treatments (Fig. 3.4c.). Their maximum number occurred at DAP 63 (72.9^{d} larvae per flower without NPK, 66.5^{d} with NPK). As for adults, *Senna* mulch yielded the highest number (32.5^{d}), which was marginally more than for the control (26.3^{d}) ($P \geq 0.05$). *Imperata* mulch was in between. The trend between fertilized and non-fertilized plots diverged significantly in favor of NPK^{-} treatments, which proceeded at a lower level ($F = 3.2^{[l]*}$) (Fig. 3.4d.). A plateau-like maximum was recorded from DAP 56 to DAP 63, which accounted for most of the excessive abundance. Before and after this plateau numbers were low. At the maximum levels DAP 56 and DAP 63, fertilized plots counted 121.7^{d} and 120.5^{d}, respectively, compared with blank plots with 88.3^{d} and 95.5^{d} for the two DAPs.

Fifth season (I/97)

Maruca vitrata. Larval numbers were not influenced by treatment application (Fig. 3.5b.). The peak at DAP 56 revealed 9.6^{d} larvae per 20 flowers.

Megalurothrips sjostedti. Larvae and adults kept developing in a different way over time although they were not different in level across time ($F = 14.7^{**}$). Both stages peaked at DAP 63. Mulch had a general impact on larvae across time, with the control suffering lowest attacks (10.8^{d}) and *Senna* the highest (14.2^{d} larvae per flower) ($F = 3.8^{*}$) (Fig. 3.5c.). *Imperata* mulch was in between (12.5^{d}). Adult counts were significantly higher across time in all fertilized treatments ($F = 4.1^{*}$), with a mean of 8.5^{d} compared with 7.3^{d} for blank plots (Fig. 3.5c.). These variations in abundance were accompanied by similar density indexes.

Lema

First season (I/95)

Maruca vitrata. Abundance of *M. vitrata* did not change due to treatments. The population peak occurred at DAP 49, with 5.8^{d} larvae per 20 flowers (Fig. 3.6b.).

Megalurothrips sjostedti. A comparison of the two stages, larvae and adults, indicated an overall difference in abundance ($F = 15.4^{**}$). Larval numbers (5.5^{d}) were double those of adults, which averaged 2.6^{d} organisms per flower. Both stages also behaved differently over time throughout the season ($F = 13.2^{[q]**}$) (Fig. 4.6c,d.). Larval numbers did not show differences due to treatments. Their numbers increased fast to a plateau during DAP 49 and DAP 56, with mean numbers (across NPK treatments) of about 12.6^{d}, and dropped fast at DAP 63 (Fig. 3.6c.). The adult population started more slowly and had a comparatively lower plateau one week later at DAP 56 and DAP 63 (Fig. 3.6d.). Their peak across NPK levels was around 5.0^{d}. The population remained at this level when flowering ceased one week later. Variation among treatments was not discovered. Densities remained similar among stages and treatments.

Second season (II/95)

Maruca vitrata. Treatments did not affect *M. vitrata*, although Fig. 3.7b. suggests slightly more larvae in fertilized plots. A climax at DAP 49 attracted on average 2.7^{d} larvae per 20 flowers in the blank plots against 3.5^{d} for fertilized ones. Differences on the density index principally followed an effect due to fertilizer. Plots with applied NPK recorded higher densities than non-fertilized plots across time ($F = 4.4^{*}$).

Megalurothrips sjostedti. Larval and adult numbers were distinct at levels across time, with very low numbers for larvae ($F = 22.0^{**}$) (Fig. 3.7c,d.). Trends demonstrated an obvious difference as well, larvae starting with a much higher abundance than adults ($F = 9.8^{**}$). For larvae and adults separately, no impact was attributed to treatments. Adults were present in relatively high numbers even at the first sampling event (DAP 49) with 61.2^{d} organisms per flower (across NPK levels), sharply decreasing afterwards. Larvae followed the same patterns

but at a much lower level, not exceeding 20.4[d] at DAP 49. The respective density indexes did not vary significantly.

Third season (I/96)

Maruca vitrata. Abundance patterns for the control differed from mulch on NPK levels ($F = 4.8^{*}$). Whereas in non-fertilized plots the control yielded significantly lower numbers of *M. vitrata* than *Imperata* (*Senna* remained in between), the control was significantly more preferred than *Senna* within fertilized plots (*Imperata* being intermediate). *Senna* without NPK was thus close to both the control and *Imperata* with fertilizer. *Senna* without NPK also counted at the maximum (DAP 49) double the number as for *Senna* with NPK, the control, and *Imperata*, the latter two without NPK (Fig. 3.8b.). Trends did not reveal significant differences. These abundance patterns were accompanied by similar density indexes.

Megalurothrips sjostedti. Comparisons of larval dynamics against adults resulted in significant variation of profile levels ($F = 9.3^{**}$) as well as of profile shapes ($F = 16.5^{**}$) (Fig. 3.8c,d.). Larvae showed differences in profiles in favor of non-fertilized plots, where fewer numbers were counted ($F = 2.6^{*}$) (Fig. 3.8c.). The peak at DAP 56 was higher in fertilized plots (56.1[d] larvae per flower) than in blank plots (42.5[d]). A short crossing-over occurred at DAP 63, pointing to a longer high in the profile for treatments without NPK. The density index revealed that higher larval abundance in fertilized plots occurred together with increased densities in the same plots. This was significant on the linear trend ($F = 6.0^{[l]**}$) (Fig. 3.8c.). Adults displayed two peaks over time (Fig. 3.8d.), being higher for fertilized plots, but the trend did not differ significantly. Levels were different across time, indicating higher abundance for the fertilized treatments ($F = 7.5^{**}$). During the first peak, 41.5[d] adults were counted in fertilized treatments against 18.3[d] without NPK; the second peak mounted to 50.2[d] with NPK and 39.2[d] without fertilizer.

Fourth season (II/96)

Maruca vitrata. More larvae were collected in the fertilized plots across time ($F = 5.6^{*}$) (Fig. 3.9b.). A much higher count at the first sampling event (DAP 42) in these treatments (6.9[d] larvae per 20 flowers with NPK against 1.4[d]) was followed by a slim lead of these plots compared with those without NPK. The profiles obviously did not differ. The corresponding densities did not reveal significant differences.

Megalurothrips sjostedti. Population dynamics of larvae were significantly distinct from those of adults at levels ($F = 129.7^{**}$) and profiles as well ($F = 15.6^{[q]**}$) (Fig. 3.9c,d.). Larvae developed differently when fertilizer was applied ($F = 5.8^{[l]**}$) (Fig. 3.9c.). Both levels peaked at DAP 56, but the population increase was faster and reached higher levels in fertilized plots than in non-fertilized ones. NPK^{+} treatments peaked with 64.5[d] larvae per flower; plots without NPK reached 39.0[d]. As for adults, NPK profiles varied on the first order polynomial ($F = 4.3^{**}$)

(Fig. 3.9d.). Treatments without fertilizer peaked higher one week earlier (DAP 49) than those where NPK was applied (DAP 56), but the population built up earlier in NPK^{+}, and levels remained slightly higher after DAP 56. A higher density index was calculated for adults in non-fertilized plots ($F = 6.8^{*}$).

Fifth season (I/97)

Maruca vitrata. Larval numbers differed marginally on the trend between fertilizer levels ($P \geq 0.05$) (Fig. 3.10b.). Slightly more larvae were counted in fertilized plots at the beginning. At DAP 49, a maximum resulted in 5.2^{d} larvae per 20 flowers when NPK was applied and 3.8^{d} in blank plots. The density indexes remained similar for the respective treatments.

Megalurothrips sjostedti. When comparing dynamics of larvae against adults, no important variation in abundance levels was found across time. Rather, they demonstrated significant changes over time ($F = 4.1^{**}$) (Fig. 3.10c,e.). More precisely their different activities could be ascribed to the impact of mulch over time ($F = 2.4^{**}$). The larval stages were significantly distinct on NPK profiles ($F = 2.5^{*}$) (Fig. 3.10c.). Fertilized plots built up populations faster and resulted in a higher maximum (64.3^{d}) than those without NPK (55.6^{d}). After the peak, both levels moved close together. Mulch had an impact on profiles of *Senna* and *Imperata* on the second order polynomial ($F = 2.9^{[q]**}$). The two profiles were shifted by about one week, with *Imperata* earlier in population build-up. The variation in trends between the control and *Senna* was marginal on the contrasts. The kurtosis for the control was smaller than for *Senna*, the latter mounting to a higher maximum. Adults were separated on a quadratic trend between NPK levels ($F = 6.1^{[q]**}$) (Fig. 3.10e.). Fertilized plots resulted in a tendentiously faster increase, while unfertilized treatments were retarded by one week. Mulch expressed varying profiles for adults due to NPK application ($F = 1.9^{*}$). In non-fertilized plots, the control attracted highest numbers, but it remained at the lowest level when fertilized. In general, larval and adult populations collapsed to low abundance after DAP 63 but did not fall to zero weeks after harvest. The latter interaction between mulch and NPK was expressed in the same way for the density index. Treatments, which revealed higher abundance, also resulted in a higher index for both larvae ($F = 4.9^{*}$) (Fig. 3.10d.) and adults ($F = 3.3^{*}$) (Fig. 3.10f.).

IITA

First season (I/95)

Maruca vitrata. Differences due to mulch application were not recorded. However, neem peaked highest at DAP 56 with 4.4^{d} larvae per 20 flowers, and *Senna* was the lowest with 2.9^{d} larvae (Fig. 3.11b.).

Megalurothrips sjostedti. There was strong evidence of differences in trends between larvae and adults ($F = 18.0^{**}$) (Fig. 3.11c,d.). Larvae did not deviate on mulch treatments (Fig. 3.11c.). A maximum occurred at DAP 63, which was highest for neem (74.7^{d}). Right afterwards, the population collapsed to almost zero. Adults did not reveal significant variation either (Fig. 3.11d.). After a common increase to DAP 56, *Senna* and neem dropped slightly in numbers, the control remained stable, and *Imperata* steadily rose until the end of sampling at DAP 70, reaching numbers of 70.2^{d} larvae per flower. The corresponding density index did not show significant differences.

Second season (II/95)

Maruca vitrata. No variation was detected in total for the comparatively low larval numbers (Fig. 3.12b.).

Megalurothrips sjostedti. Larval and adult numbers did not differ across time but rather demonstrated significantly varying profiles ($F = 25.0^{[l]**}$) (Fig. 3.12c,d.). Larval profiles were distinct for *Senna*, in which the population grew slower and peaked at DAP 56 with 105.5^{d} larvae per flower – less than all other treatments, which reached 140.0^{d} and higher ($F = 2.0^{[q]*}$) (Fig. 3.12c.). The lower peak for larvae in the control was accompanied by a significantly higher density index in the control ($F = 3.6^{[q]**}$) (Fig. 3.12c.). Adults increased faster to their first high at DAP 49 and remained on a plateau or even declined for the control and *Senna* mulch at the time of the peak for larvae (Fig. 3.12d.). Across time *Imperata* mulch yielded significantly fewer larvae than the other treatments ($F = 7.7^{**}$).

Third season (I/96)

Maruca vitrata. Mulch application revealed differences in levels across time. The control and *Imperata*, being close in abundance, rose to a significantly higher level than *Senna* and neem mulch ($F = 4.1^{*}$) (Fig. 3.13b.). The peaks for the control and *Imperata* at DAP 56 were 5.6^{d} and 5.2^{d} larvae per 20 flowers, respectively. *Senna* and neem had a weaker climax one week earlier with 3.3^{d} and 2.6^{d}, respectively. The density index was at the same time higher for the control than for neem ($F = 2.9^{*}$).

Megalurothrips sjostedti. Larvae differed from adults in profiles ($F = 2.2^{*}$) (Fig. 3.13c,d.). Overall levels were not different. Larvae and adults separately did not show considerable variation between profiles. Larvae were attracted faster in the control with a peak one week earlier (DAP 56) than in mulch treatments (Fig. 3.13c.), except for neem mulch. *Senna* and *Imperata* plots kept higher abundance levels until the end of the season. Apart from neem, adults reached their climax at DAP 56 and decreased slowly thereafter (Fig. 3.13d.). Neem delayed the population peak for one week and was below the levels of all other treatments. The density index remained similar for all treatments.

Fourth season (II/96)

Maruca vitrata. *M. vitrata* was very rare during this season and did not show any significant difference among treatments. At DAP 63 a few larvae were found in *Senna* and neem mulch and one week later larvae were extracted out of the control only (Fig. 3.14b.).

Megalurothrips sjostedti. Both stages displayed clear variation in their overall levels ($F = 8.1^{**}$) as well as their dynamics over time ($F = 25.6^{**}$) (Fig. 3.14c,d.). Larvae in the control peaked at DAP 56 (41.7^{d} larvae per flower), but reached a much higher maximum one week later for the mulch treatments *Senna* (95.2^{d}), *Imperata* (97.1^{d}), and neem mulch (75.1^{d}) ($F = 2.8^{**}$). The densities for larvae were different between the control and *Senna* mulch ($F = 6.1^{**}$) (Fig. 3.14c.). The relationship was inverse, decreasing for the control while all other treatments rose towards DAP 63. Adults were not different on levels or trends.

Fifth season (I/97)

Maruca vitrata. Dynamics of *M. vitrata* was not influenced by the use of mulch. However, neem peaked highest at DAP 49 with 4.4^{d} larvae per 20 flowers (Fig. 3.15b.).

Megalurothrips sjostedti. Abundance patterns were different on the trend separating larval from adult dynamics ($F = 6.4^{**}$) (Fig. 3.15c,d.). Larvae demonstrated the same tendencies, which were not significantly different among treatments (Fig. 3.15c.). A common peak occurred at DAP 63 with *Senna* on top (62.8^{d} larvae per flower) and *Imperata* (52.4^{d}), neem (46.7^{d}), and the control (42.6^{d}) following. Adults were more abundant in *Senna* mulch, distinctly peaking at DAP 63 (61.8^{d}); the other profiles remained close together at a far lower level ($F = 2.3^{[q]**}$) (Fig. 3.15d.). The density index did not suggest significant differences.

Discussion

Regional differences

All regions

Maruca vitrata. The threefold higher abundance of *M. vitrata* in Lema compared with IITA could not be explained by climatic conditions alone. Although Lema was the overall warmest region, the difference of 0.4°C was too small to cause this effect. Temperature does reduce the duration of the different developmental stages and could increase the population *in situ* through shorter generation follow-up (Taylor 1967). Flower numbers in Lema did not suggest any effect, since no significant difference on average among the regions was recorded. It is rather believed that the neighboring environment strongly influenced the populations, be-

ing a vital refuge where pests maintain their permanent population and from where they start migrating into other available feeding sites, e.g., cowpea (Wolda 1988; Tamò 1991; Ananthakrishnan & Gopichandran 1993; Leumann 1994; Arodokoun 1996; Schulthess et al. 1997). In general, the diversity of alternative host plants was found to be richer in terms of number of species in Lema, consisting of more potential host plants for *M. vitrata* (Figs. 7.7.-7.17.). Particularly during season II/96, very high numbers of *M. vitrata* were collected in the alternative host *Dolichos africanus*, revealing larvae in roughly every second flower of the sample (Fig. 7.1.). The coinciding peak in cowpea at the same time suggests strong interaction between both host plants. *D. africanus* served as the resource from where migration into cowpea originated. It is suggested that the population size might be influenced principally by the surrounding alternative hosts and secondly by the flowers available in the cowpea field.

Across seasons Tokpa/Ayou recorded most flowers and biggest plants (although not significant in effect), followed by Lema and IITA, which were relatively close together. The phenological potential (number of reproductive nodes + associated number of flowers) of Tokpa/Ayou (Summerfield et al. 1983; Summerfield & Roberts 1983) thus was highest but it did not account for a respectively higher population. Most larvae of *M. vitrata* in cowpea occurred in Lema, which had lower potential but a more diverse host environment. During seasons II/95-I/97, *M. vitrata* was more abundant in Lema compared with Tokpa/Ayou. There was again no overall indication of phenological influences in cowpea, therefore external causes probably led to this difference. In Lema eight alternative host plants for *M. vitrata* were found, five of which flowered during both cropping seasons, one in the early seasons, and two in the late seasons. In Tokpa there were four host plants besides cowpea where *M. vitrata* was collected; two of these flowered in both seasons and two in the early rainy season only. Apart from the number of species, the higher number of plants flowering during both seasons in Lema created a more stable environment, where *M. vitrata* could maintain its population apart from the changing patterns in cowpea cultivation. Higher numbers of *M. vitrata* during season I/97 in Tokpa/Ayou compared with IITA are probably the result of significantly higher flower numbers in Tokpa/Ayou, serving as more favorable source for feeding and subsequent population build-up. During the early cropping seasons, *M. vitrata* was found more often in flowers. In parallel, the amount of rainfall was more elevated in these seasons. Flower numbers were also tendentiously higher and thrips populations were significantly lower in all first seasons. Lower precipitation during the late seasons seems to be more favorable for thrips (Hurst 1964; Lewis 1964; Lewis 1973; Ezueh 1981) and together with the increasing accumulation of thrips populations during the year the flower shedding is considerable. This dominant influence by thrips reduces the food source for *M. vitrata.* This complicates the real picture of damage by *M. vitrata* (Taylor 1967), a phenomenon Jackai & Singh (1991) called a masking effect.

Lema recorded much higher densities than IITA, while plants in both regions did not vary greatly in size or flower output and therefore phenological potential. This was due to remarkably higher numbers of *M. vitrata* per flower in Lema. Lema resulted also in higher densi-

ties than Tokpa/Ayou, which had only slightly higher larval abundance. The “dilution effect” of more flowers on more nodes in Tokpa/Ayou led to relatively lower numbers on *M. vitrata*.

Megalurothrips sjostedti. Larval and adult abundance, which did not vary in pattern from each other, was significantly lower during season I/95 in Lema compared with both other regions and in parallel recorded significantly lower flower numbers. Lema had higher and regularly occurring precipitation in contrast to Tokpa/Ayou and IITA, which probably kept off the thrips and allowed a very early flower maximum when the rains decreased in amount (Fig. 2.10.). A sudden drop in precipitation led to a peak in larval numbers, probably reducing the number of flowers through increased shedding. No potential alternative host plants were found in the neighborhood around the time of planting or flowering, hence the potential for adults migrating into cowpea was minimal. Regular rains did not allow strong adult migration and the population therefore remained at very low levels, with increases mainly resulting from the larvae produced in the cowpea fields. In season II/95 IITA resulted in significantly highest thrips numbers probably on the basis of higher flower numbers in this region. The plants were bigger, too, resulting in a higher phenological potential (Summerfield et al. 1983; Summerfield & Roberts 1983) and thus higher overall flower numbers. The alternative host plants in the neighborhood indicated a more or less similar migratory pressure in terms of number and potential for thrips development in these species. A different effect from this point of view can be excluded. In season I/96 Tokpa/Ayou revealed lowest thrips numbers compared with both other regions. At IITA there was no important alternative host plant present (Fig. 7.14.) and in Lema this was the short flowering *Afrormosia laxiflora* (Fig. 7.9.) with low thrips numbers per flower.

In Tokpa/Ayou *Centrosema pubescens* flowered throughout the long dry season and maintained moderate thrips levels into the flowering phase of cowpea (Fig. 7.4.). This would have suggested a comparatively higher thrips abundance in Tokpa/Ayou, which did not occur. Flower numbers of cowpea were also similar to those in Lema, indicating no shortage in resources. In this region precipitation was highest right at flowering peak (DAPs 49, 56) (Fig. 2.7.), possibly strongly affecting the migration into cowpea from the neighboring alternative hosts. This migration was delayed by rains. When migration was possible during a drop in precipitation, flower numbers in cowpea were at a low level already, limiting the resources for a favorable population build-up. The population therefore remained small.

Adults remained at the lowest level during season II/96 at IITA. This was obviously the result of very low rainfall (<100 mm), being more than half of the amount of the other regions. This severe stress led to smallest plants and lowest flower numbers, which were strongly limiting conditions for successful population development for thrips. As for season I/97 thrips abundance was highest in Lema. Overall precipitation was lowest in Lema, and right at the flower peak (DAP 49) precipitation approached zero. This obviously encouraged immediate migration of thrips adults into cowpea (Fig. 3.10.) from the neighboring host plants of the species *Tephrosia bracteolata*, which maintained considerable levels of thrips over weeks, starting around the sowing date (Fig. 7.11.). Larvae were found in cowpea flowers in high numbers

one week before flower peak, causing a respective flower shedding and keeping subsequent larval levels low over several weeks. The other regions experienced higher precipitation at the time of flowering, delaying the abundance peak of thrips (Figs. 4.5., 4.15.). Rains, which coincided with early flowering, reduced damages to reproductive parts.

In season II/96, Lema showed highest densities together with higher flower numbers than IITA and slightly less than in Tokpa/Ayou. Adult numbers were slightly higher than in Tokpa/Ayou but much more elevated than at IITA. This allows the conclusion that flowers in Lema were indeed more densely populated than in the other regions in this season.

On-farm regions

Maruca vitrata. Larvae of *M. vitrata* were found more frequently in fertilized treatments probably mainly due to the better nutritional quality of the plant tissue after NPK application. Herbivorous insects have been proved to recognize different nutritional patterns and develop respective preferences (Fennah 1963; Bentz et al. 1996; Mollema & Cole 1996). Results show a direct correlation between the levels of N_2 and the extent of infestation (Painter 1951; Southwood 1973; Scriber 1984). This might also come about by an enhanced egg production (White 1984), which directly increases the population. There were slightly more flowers in fertilized treatments, although not significantly so, creating a better resource for oviposition and feeding (Taylor 1978; Arodokoun 1996).

Megalurothrips sjostedti. Thrips' abundance did not significantly increase with fertilizer application, although a slight positive tendency towards NPK plots was observed. A nutritional effect due to N_2 levels in the plant, which was proposed by Painter (1951), Southwood (1973), Scriber (1984), Bentz et al. (1996), and Mollema & Cole (1996), might account for this phenomenon.

Seasonal differences within the same region

Tokpa/Ayou

Maruca vitrata. Season I/95 revealed the highest larval numbers (Table 3.4.). Precipitation patterns were very variable among seasons and did not furnish an explanation (Table 2.2.). Thrips abundance in total was also not lowest in season I/95 (Table 3.5.) and peaked generally late (DAP 63) in all seasons except for season II/96, which recorded its peak one week earlier (Fig. 3.4.). This would have allowed *M. vitrata* to build up a population undisturbed by flower shedding caused by thrips in all seasons except for season II/96, which, in fact, did not occur. Flower numbers in cowpea were even higher in season I/96 without strong implications for larval populations of *M. vitrata*. The host plant composition in the neighborhood was particu-

larly poor in this season, not suggesting any stimulating influence through alternative habitat resources (Fig. 7.2.). However, the influence is believed to originate from alternative host plants that were out of reach during the limited regular screening around cowpea fields, allowing adult *M. vitrata* to invade cowpea fields. Larvae were never found in this region in alternative host plants during the permanent sampling. An estimation of how far the particular environment was responsible for maintaining a population outside the cowpea fields therefore was not feasible. Season II/96 resulted in lowest larval counts of *M. vitrata*. Flower numbers were lowest in this season and accompanied by the smallest amount of rainfall, which generally did not create favorable conditions for high reproduction. Stronger influence is suggested by thrips numbers (Table 3.7.), particularly adults, and their peak abundance (Fig. 3.4.), which steeply rose during one week towards DAP 56. This invasion with following oviposition possibly led to high flower shedding in addition to the already low flower numbers, evidently discouraging and subsequently suppressing population set-up of *M. vitrata*, which depends on the same resources. All first growing seasons yielded higher counts of *M. vitrata*, while thrips numbers were significantly lowest. These patterns in thrips distribution allowed a better population build-up of *M. vitrata* during all early rainy seasons while suppressing it later in the year.

Megalurothrips sjostedti. Larvae and adults were more abundant in all late cropping seasons. Thrips accumulate throughout the season (Tamò et al. 1993b) as sowing dates are delayed, increasing pest pressure (Summerfield et al. 1974). Season I/96 resulted in lowest larval and adult numbers despite being in parallel with highest flower numbers. Precipitation was the second highest after season I/97 but the distribution around the flower peak probably protected the plant from early and high thrips attacks. More than 100 mm during the week before DAP 35 and again roughly 100 mm two weeks later – right at the flower peak – obviously kept off thrips efficiently. Highest flower numbers thus were possible. When rainfall decreased and migration became possible, flower production had already dropped and no longer provided good feeding resources. Adult migration remained low and the population rather developed from within the cowpea field as low adult abundance and a peak of larvae at DAP 63 suggested (Fig. 3.3.). In all other seasons population build-up was less disturbed by adverse climatic conditions. Larvae occurred in highest numbers in season II/95, which recorded second lowest precipitation and had significantly highest temperatures. The low precipitation facilitated migration of adults from alternative hosts to cowpea. The high temperatures (due to daily maximums) increased the take-off rate, leading to a high proportion of volatile adults (Lewis 1973), which did not result in high numbers in the flowers but possibly rather in abundant oviposition.

Adults were most numerous in season II/96. Temperature was lower than in season II/95 and precipitation was even lower. Migration was very strong (Fig. 3.4.), but due to slightly lower temperatures the proportion of volatile adults was lower, thus increasing the number of organisms remaining in flowers. At the moment of sharp increase of adult numbers in cowpea flowers *Cajanus cajan* was discovered flowering in the neighborhood (Fig. 7.5.) counting con-

siderable adults' numbers, too, the migration of which might have suddenly infested the nearby cowpea, which was in its stage of peak flowering (DAP 49). Density patterns as indicated by the index between early and late cropping seasons appeared straightforward from abundance of thrips. Since all early seasons revealed fewer thrips and recorded lower densities than late seasons but no significant variation was found in flower numbers, this effect is directly attributable to increased thrips numbers. The same patterns applied for adults in season II/96, indicating that higher numbers combined with higher densities accounted for real season effects.

Lema

Maruca vitrata. Larval abundance was generally higher in fertilized treatments in accordance with slightly higher flower numbers in these treatments, except for season I/97, when non-fertilized treatments revealed more flowers. A higher suitability in terms of nutrients in the plant was believed to be the main reason for higher feeding preference and higher egg productivity on fertilized plants (Painter 1951; Fennah 1963; Southwood 1973; Scriber 1984; White 1984; Bentz et al. 1996; Mollema & Cole 1996). Within fertilized plots season I/96 counted more larvae than seasons II/95 and I/97. Since this season recorded the highest rainfall amounts and also led significantly in flower production, this combination was suggested as having accounted for this effect. Fertilizer probably became available faster and in higher concentrations, resulting in better uptake by the plants before the remainder leached into the deeper soil layers.

Megalurothrips sjostedti. Seasons I/96 and I/97 were leading in larval numbers compared with seasons I/95 and II/95 (Table 3.7.). At the same time flower numbers were highest in the same two seasons, possibly resulting in a higher carrying capacity (Tamò et al. 1993b) and being more attractive while offering better feeding and oviposition sites (Table 2.9.). As for adults, season II/96 revealed highest counts compared with seasons I/95, II/95, and I/97, obviously due to a highly diverse and potential habitat of alternative host plants (Fig. 7.10.) carrying very high numbers particularly of adults throughout the cowpea growing period. A high migratory pressure into cowpea was expected from this natural environment. Season I/95 in turn had lowest adult numbers in parallel with lowest flower production and a poor host plant environment (Fig. 7.7.). Except for *Afrormosia laxiflora*, which had a short flower period of three weeks well before sowing of cowpea and carried high larval but low adult numbers, no real host plant was found until early flowering of cowpea. The limited migration together with a low carrying capacity in flowers of cowpea did not allow an important population build-up.

Higher densities in season I/97 than in II/95 were the result of significantly more larvae in I/97 despite slightly more flowers in that season. This indicates that the variation between the two seasons is attributable to a real difference in abundance of thrips larvae. Adults showed highest densities in season II/96, which also had significantly the highest adult abundance but

relatively low flower numbers. A concentration effect due to fewer flowers is more likely to explain the variation than more adult thrips in total. Season I/97 also yielded higher densities on the basis of by far higher adult abundance but similar flower numbers. This indicates indeed a real difference in abundance.

IITA

Maruca vitrata. More larvae were counted in flowers during seasons I/95 and I/96 than in seasons II/95 and II/96. More flowers were also found in the same two early seasons in parallel with more precipitation. Considerable rainfall was measured before and right at the time of peak flowering in seasons I/95 and I/96, so that thrips migration was probably suppressed, allowing better flower production and therefore more favorable conditions for *M. vitrata* (Arodokoun 1996) (Figs. 3.15., 3.17., 4.11., 4.13.). Seasons II/95 and II/96, in turn, had lower flower numbers and much higher thrips levels at flowering, which was not protected by concurrent rainfall (Figs. 3.16., 3.18., 4.12., 4.14.). Early cropping seasons revealed higher numbers of *M. vitrata* than late ones. This effect might have arisen from on average more flower numbers, higher precipitation, and lower thrips numbers in these seasons. Alternative host plants in the neighborhood were more diverse and carried higher thrips numbers in late seasons augmenting migratory pressure into cowpea fields and resulting in more damage to flowers (Taylor 1964; Singh & van Emden 1979; van de Klashorst & Tamò 1995), which are also a basic resource for *M. vitrata* (Ghesquière 1942; Taylor 1967; Taylor 1969; Taylor 1978; Woolley & Evans 1979; Tayo 1988; Atachi & Ahohuendo 1989; Firempong & Magalit 1990; Tamò et al. 1993b).

Season I/96, which was more densely populated than season II/96, confirms a real difference in infestation, although flower numbers were higher in season I/96, too. Since larval abundance was also higher in I/96, the dilution effect through more available resources (flowers) was compensated by a higher larval abundance.

Megalurothrips sjostedti. Thrips larvae and adults were more abundant in seasons I/95 and II/95 than during II/96 and I/97. Precipitation did not suggest the pattern needed to confirm this effect since it varied strongly in both clusters. Seasons I/95 and II/95 counted more flowers, attracting more adults and leading to higher oviposition, which explained the higher larval numbers in the same two seasons. At the same time, migratory activity was stronger because of the presence of potential alternative host plants in the neighborhood and moderate to high thrips levels in these plants (Figs. 7.12., 7.13.). The very high larval and adult abundance during season II/95 can mainly be explained by the higher diversity in alternative hosts and the elevated infestation, particularly of adults, the number of which steeply increased when cowpea started flowering (Fig. 7.13.). Season I/96 was not different from seasons II/96 and I/97 for larvae but revealed higher numbers of adults. The first three seasons (I/95, II/95, I/96) counted more flowers than the remaining two seasons and possibly attracted more adults migrating into

cowpea, but oviposition probably was limited in season I/96 despite high adult numbers. Right at peak flowering (DAP 49) (Fig. 2.17.) a strong rainfall peak was also recorded, which delayed adult migration into cowpea (Fig. 3.13.). When migration became possible due to ceasing rainfall, incoming adults met decreasing flower development, which was no longer favorable for strong oviposition. Season II/95 also attracted more adults than season I/96, the latter having the highest precipitation among all five seasons and an almost non-existent alternative host range; the combination did not allow a strong population build-up and subsequent migration was obstructed by high rainfall.

Adults recorded significantly the highest density index in season II/95. Since their abundance was also significantly higher than in seasons II/96 and I/97 and at least marginally higher than in seasons I/95 and I/96, the seasonal effect was confirmed. This resulted despite higher flower numbers in season II/95, thus proving a real abundance difference.

Differences within seasons

Tokpa/Ayou

First season (I/95)

Maruca vitrata. There was a clear trend for larvae to favor fertilized plots (Fig. 3.1.), which also recorded higher flower numbers (Fig. 2.5.). As was the case for flowers, the larval peak in fertilized treatments occurred slightly earlier and fell sharply, declining as steeply as it rose. Since thrips peaked one week later than *M. vitrata* and two weeks after flower peak, flower numbers reached a comparatively high maximum (Chapter 2). Flower shedding due to thrips attacks was thus reduced. This difference in levels between fertilized and non-fertilized plots was a direct reaction to flower numbers following the same pattern, which offered better resources for larval exploitation (Taylor 1978; Arodokoun 1996). On the other hand, larvae followed an indirect effect through more nitrogen-rich tissue, which is softer and increases availability of basic elements (e.g., enzymes) for larval development (Lewis 1973; Ananthakrishnan & Gopichandran 1993; Bentz et al. 1996; Mollema & Cole 1996). The difference in trend for flowers and larvae, meaning a faster increase and subsequent drop in profile, is attributable to faster senescence of the plants when they received fertilizer (Summerfield et al. 1978; Wien & Tayo 1979; Wien & Summerfield 1984).

Since the fertilized treatments did not show a higher density index, the effect was rather due to increased flower numbers in these treatments attracting more larvae and possibly less caused by increased nutritional suitability.

Megalurothrips sjostedti. Thrips abundance followed the patterns of flowers, which marked a relationship between mulch and chemical fertilizer (Chapter 2). As was the case for flowers, thrips in total revealed higher numbers in the control than *Senna* mulch without NPK, but fewer thrips were yielded in the control than *Senna* and *Imperata* mulch when fertilizer was applied. This interaction in favor of NPK plus mulch arose possibly because fertilizer application increased the nutrient content of the soil and mulch retained more humidity in the soil, decreasing losses due to leaching. The higher humidity and organic matter through beginning decomposition of mulch favored nodulation and activities of soil fauna (Masefield 1957; Terada 1971; Rachie & Roberts 1974; Müller-Sämann & Kotschi 1997), which, on the basis of nitrogen nutrition, accelerated the availability of soilborne nutrients. The fact that without mulch the control was more preferred by thrips and had slightly lower flower numbers as well may be explained by the fixation effect of nutrients through newly applied mulch (Hagihara 1975). This was compensated for in the fertilized plots. Larvae were distinct on the profiles for fertilizer, the peak of which in the fertilized plots was higher and dropped faster (Fig. 3.1.). Like *M. vitrata* larvae, this phenomenon was ascribed to faster availability of applied nutrients followed by a faster senescence of fertilized plants. The direct and indirect effects on thrips populations in terms of nutrition followed as described for *M. vitrata*. Whereas the visible but slight differences for adults were not significant, the significantly higher larval numbers pointed to higher oviposition in fertilized treatments based on better suitability.

Non-significant differences in densities suggested that the NPK*mulch interaction as well as the fertilizer main effect were the result of higher flower numbers with a higher carrying capacity rather than real treatment effects.

Second season (II/95)

Maruca vitrata. No significant variation was found although visible investigation pointed to a slightly higher preference of *Senna* than the control and *Imperata* without NPK and less attractive influence of *Senna* compared with the control and *Imperata* with fertilizer.

Imperata showed a higher density index than *Senna*, both combined with fertilizer. *Imperata* in this case revealed fewer flowers and slightly more larvae. It can therefore be assumed that *Imperata* was not more infested than *Senna*. A concentration effect was held responsible.

Megalurothrips sjostedti. Larvae and adults were not influenced by treatments. Larvae remained in total lower in numbers than adults (Fig. 3.2.), indicating a weak population build-up due to dry conditions resulting in fewer flowers. At DAP 63, when flower production was at its maximum (Fig. 2.6.), the adult population also reached its peak. This was enhanced as precipitation ended and temperatures increased (due to higher maximums), resulting in a higher take-off and migration rate (Lewis 1973) and larger available populations, particularly adults, in alternative host plants in the vicinity of the cowpea plots (Fig. 7.3.). Since the flower numbers decreased and plants had aged already, oviposition did not occur in high numbers, as is confirmed by low larval numbers.

Third season (I/96)

Maruca vitrata. This was the season with second highest precipitation (>400 mm) (Table 2.2.). Neither abundance nor densities varied among treatments. No differences in flower numbers were found. Precipitation reached a high peak during the week towards flower peak (Fig. 2.7.), resulting in low advantage of these plots compared with blank ones. The high rainfall probably caused considerable leaching in fertilized plots. However, a slight tendency in favor of fertilized plots was suggested from Fig. 3.3., larvae being more abundant in these plots. Assessing the trend showed an earlier increase in fertilized plots, which was confirmed by higher densities. Since flower numbers were barely deviating, this marginal effect is to be ascribed directly to nutritive patterns and increased female productivity (Painter 1951; Lewis 1973; White 1984; Bentz et al. 1996; Mollema & Cole 1996).

Megalurothrips sjostedti. Whereas larvae responded marginally to fertilizer, adults showed the same trend significantly. Although not significant, the density index was higher in fertilized plots, too. The larval peak occurred late, at DAP 63, and adults again one week later – obviously restrained by a high rainfall peak at DAP 49 the time of main flowering. Precipitation was very high in this season, and the mostly cloudy weather and lower temperatures, which dropped towards the end of the season (Fig. 3.3a.), did not create favorable climatic conditions for adult thrips to migrate in large numbers from the alternative host *Centrosema pubescens,* which carried moderate thrips levels (Fig. 7.4.). Again, the variation between fertilizer plots is believed to stem from nutritive effects, since flower numbers were almost congruent, as was reported for *M. vitrata*.

Fourth season (II/96)

Maruca vitrata. A marginal NPK effect recorded fewer larvae in fertilized treatments possibly due to much higher numbers of adult thrips, which might have caused considerable flower shedding. The fact that flowers were not higher in fertilized treatments could be the result of high flower shedding on initially higher numbers in fertilized treatments. An interaction occurred between NPK and mulch, with the result that larval numbers in the control increased when fertilizer was applied but decreased in both mulch treatments due to NPK application. The increase in the control can be explained by a higher carrying capacity (Tamò et al. 1993b) in fertilized plots, since plants were bigger and had more flowers, and thrips numbers were higher as well. The decrease in *Senna* followed a decrease in flower numbers and in larval thrips numbers, and an increase in adult abundance. With the reduced flower numbers the higher adult numbers possibly had a more damaging impact on the availability of resources also needed for *M. vitrata*. In the *Imperata* treatment an increase of larvae of *M. vitrata* would be expected on the basis of bigger plants, more flowers, and generally reduced thrips numbers in fertilized plots. The contrary was the case. This decline in pest numbers on the basis of more available resources (flowers) could not be explained with the recorded measurements. Soil

humidity, missing plants, and plant phenology, as well as population densities, did not reveal any information that could support these findings. Densities confirmed the higher larval abundance of *Imperata* treatments without fertilizer consisting of the ratio between highest abundance and second lowest flower numbers.

Megalurothrips sjostedti. While larvae did not respond to treatments, adults were remarkably more abundant in fertilized treatments although flower numbers were found not to differ. Higher shedding in these treatments might have reduced initially higher numbers, which attracted more adults than non-fertilized plots. Although not significant, *Senna* attracted slightly more adults than the control while in parallel *Senna* recorded highest flower numbers. The steep increase in the adult population to extreme levels was the result of alternative host plants in the neighborhood, mainly *Centrosema pubescens* and *Cajanus cajan*, which offered an important potential at the time of flowering. In particular *C. cajan*, which was discovered flowering within one week of peak flowering of cowpea but probably already had flowers before, seemed to have contributed to a remarkable population build-up and strong migration at the same time (Fig. 7.5.). The peak of adults was delayed slightly, possibly by rains, which occurred towards the flower peak. Larval maximums followed one week later but did not reach the levels of adults due to declining flower numbers, indicating plant senescence. The slightly higher densities at DAP 63 for adults were the result of higher adult abundance given a similar number of flowers.

Fifth season (I/97)

Maruca vitrata. The differences in preference between non-fertilized and fertilized treatments were barely visible. This season recorded the highest precipitation among the five seasons in Tokpa/Ayou, possibly leading to considerable losses through leaching of nutrients especially in the fertilized plots. Heavy rains can also lead to mechanical shedding of flowers (Tamò, pers. comm.). Flower numbers therefore were lower in these plots but generally high numbers of *M. vitrata* probably rather responded to nutritional influences of fertilizer (Lewis 1973; Scriber 1984; White 1984; Bentz et al. 1996; Mollema & Cole 1996). Densities were slightly higher in the control compared with mulch treatments, reflecting barely higher larval abundance and scarcely fewer flowers in the non-mulch treatment. A concentration effect was rather the cause of this slight difference.

Megalurothrips sjostedti. Larvae were found in higher numbers in *Senna* than in *Imperata*, which was also more than in the control. This followed congruent patterns in flower production, which nevertheless was not significant. Adults were more abundant in fertilized plots (Fig. 3.5.). The abundance was obviously not guided by flower numbers, which did not differ significantly (Fig. 2.9.), and was rather believed to be due to nutritive effects. The slightly higher flower number at DAP 49 in fertilized plots was reflected to a limited extent in adult preference at the same day where it showed a short first high. However, the difference was so little that any biological meaning can be disregarded. Adults did not vary in density, suggesting

a treatment effect since flower numbers in fertilized plots were not significantly different from those in non-fertilized plots.

Lema

First season (I/95)

Maruca vitrata. Variation in abundance and density of larvae did not occur. A relatively high number was recorded since thrips did not occur in important numbers and despite relatively low flower numbers.

Megalurothrips sjostedti. As with *M. vitrata,* no treatment differences were found for either larvae or adults of thrips. Adults represented about half the size in population than larvae did (Fig. 3.6.). Except for *Afrormosia laxiflora*, which stopped its short flowering cycle before cowpea was sown, no potential alternative host plant occurred in the neighboring fallow. Together with regular rains towards flowering of cowpea, the low external pressure together with unfavorable take-off conditions (Lewis 1973) resulted in very few adult numbers in cowpea. Flower numbers, which dropped to low levels after DAP 42, did not favor important oviposition, and larvae also remained at relatively low levels. Densities as well did not suggest differences.

Second season (II/95)

Maruca vitrata. Fertilizer plots caused a marginal positive response by larvae, probably following a better nutritive suitability (Lewis 1973; Southwood 1973; White 1984; Bentz et al. 1996; Mollema & Cole 1996). Since densities were also higher given a similar number of flowers, the nutritional effect seems to be realistic.

Megalurothrips sjostedti. Larvae and adults did not differ on levels nor did they in trends. Larvae remained much lower than adults in this season (Fig. 3.7.). A high population in alternative host plants accompanied the growing cowpea, in particular *Tephrosia bracteolata* and *Cochlospermum planchoni*, which contributed to the adults' migration into cowpea when flowers appeared at DAP 49 (Fig. 7.8.). Oviposition on already aging plants with decreasing flower numbers was not important and so the larval numbers remained low. Marginal effects on density were the outcome of no significant difference in larval numbers but in total slightly fewer flowers in fertilized treatments and a slightly higher abundance of adults in fertilized plots.

Third season (I/96)

Maruca vitrata. Without applied fertilizer, the control recorded fewer larvae than mulch, in particular *Imperata,* whereas in combination with NPK the control counted most larvae

compared with mulch, in this case particularly *Senna*. The control developed fewer flowers both with and without NPK and therefore did not support these findings on the basis of available resources. Plant growth (Chapter 2) tendentiously corresponded with larval numbers, although not significantly; the smallest plants were in the control without fertilizer and the biggest plants were in the control with fertilizer. Larval numbers of thrips tended to behave in a similar way as larvae of *M. vitrata*, therefore not being an influencing factor due to flower damage. However, there was no indicator that explained this phenomenon of larval abundance. The densities were higher in non-fertilized plots due to slightly fewer larvae in these treatments in combination with significantly lower flower numbers. This indicates that the increase in flower numbers after fertilizer application did not result in a considerable increase in the larval population, as the density index remained lower in NPK plots.

Megalurothrips sjostedti. Larvae and adults were found more often and in higher densities in fertilized treatments. This points to an increase in population on the basis of more available flowers and possibly also to a better nutritional quality in fertilized plots (Fennah 1963; Lewis 1973; White 1984; Bentz et al. 1996; Mollema & Cole 1996). Adults invaded the fields early at DAP 42, one week before peak flowering (Fig. 3.8.), although no potential alternative host plants were identified in the vicinity. They possibly were transported by wind from plants out of reach for sampling. At this time moderate numbers of *M. vitrata* larvae were already present in flowers. The following week thrips numbers declined while *M. vitrata* larvae strongly increased. These high levels of *M. vitrata* possibly caused remarkable damage to the reproductive parts enclosed in the sepals, since one larva needs four to six flowers to reach its pupal stage (Taylor 1978). Although these flowers were counted as still present (Fig. 2.12.), the interior damage probably excluded further exploitation by adult thrips, which feed on flowers, too. When flower numbers decreased at DAP 56, larvae of *M. vitrata* migrated to pods to finish their life cycle (Taylor 1978), thus leaving later flowers for thrips to feed and oviposit on.

Fourth season (II/96)

Maruca vitrata. Already high larval numbers were recorded at DAP 42 in fertilized treatments probably due to more favorable nutritive conditions (Lewis 1973; Bentz et al. 1996; Mollema & Cole 1996) rather than to differences in flower numbers, which developed distinctly one week later. A considerable pressure was assumed to stem from *Dolichos africanus*, which recorded slightly more larvae than cowpea at DAP 49, being roughly more than one larva per two flowers (Fig. 7.1.).

Megalurothrips sjostedti. Larvae and adults responded positively to fertilizer application because of the higher flower numbers in the same plots (Fig. 2.13.) and a supposed nutritive effect (Fennah 1963; Lewis 1973; White 1984; Bentz et al. 1996; Mollema & Cole 1996). Since precipitation was not very high and until DAP 35 of no importance, fertilizer allegedly dissolved slowly providing a continuous nutrient flow for plants, which in this particular case

perhaps aged later than the non-fertilized plants. The adult maximum in plots without NPK was recorded right after the rains ceased and was temporarily higher than adult numbers in fertilized plots.

As was recorded for *M. vitrata*, a rich diversity of alternative host plants with very high adult abundance made up a strong pressure potential (Fig. 7.10.) inundating flowers of cowpea. Larval density indexes separated after DAP 56, when the larval population collapsed in fertilized plots. Their index dropped accordingly since flower numbers decreased only slowly. Adults reflected slightly higher abundance given almost double the numbers of flowers in fertilized plots at the peak of DAP 49, which resulted in a lower density in these treatments. Therefore, the higher numbers in fertilized numbers are principally attributable to more flowers slightly diluting the population.

Fifth season (I/97)

Maruca vitrata. Although not significant, larvae were slightly more abundant in fertilizer treatments. Since flower numbers were similar for the different treatments, a nutritive effect was assumed (Painter 1951; Lewis 1973; Bentz et al. 1996; Mollema & Cole 1996). Lower densities within fertilized treatments in the control consisted of generally higher flower numbers in the control and lower larval abundance; densities within non-fertilized plots did not suggest an important variation.

Megalurothrips sjostedti. NPK treatments were preferred by larvae and adults resulting in early population build-up, and for larvae a higher peak, which occurred one week earlier than in non-fertilized plots. Since flower numbers were still close together at DAP 42 when the profiles between fertilized and non-fertilized separated, availability of resources could not be the reason. Very high rainfall occurred at DAP 21 (Table 2.4.), probably leading to the activation of applied fertilizer, which attracted thrips earlier than non-fertilized plots due to the higher availability of nutrients (Fennah 1963; Lewis 1973; White 1984; Bentz et al. 1996; Mollema & Cole 1996). The faster senescence of fertilized plants possibly led to a drop in abundance, reducing the nutritive suitability. Adults showed a different response to mulch due to fertilizer use. Without application of NPK, they were more abundant in the control compared with mulch treatments. In the same treatments slightly more flowers were recorded; the greater availability of resources could partly be the reason for higher preference. In fertilized treatments, adults were more attracted by mulch treatments in spite of higher flower numbers in the control. Fertilized plots measured lower soil humidity in parallel. Adults were possibly attracted more by favorable conditions for their offspring, since they pupate in the soil litter (Taylor 1967; Lewis 1973; Rösingh 1980; Mollema & Cole 1996) than by availability of resources. Given the drier soil conditions, mulch probably turned out to offer the humidity conditions needed for successful pupation (Mollema & Cole 1996). Larval numbers followed this trend, although not significantly, indicating that this could be a reason. Densities for larvae and adults together were lower in fertilized plots in the control with concurrent higher flower

counts. This suggested a dilution effect of the population rather than a real treatment influence. Within non-fertilized plots, higher thrips numbers were recorded in the control on slightly higher flower numbers. Since the difference in flowers was very small and non-significant but thrips numbers were significantly higher, the effect was considered to be real.

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First season (I/95)

Maruca vitrata. Differences due to treatments were not suggested as was the case for densities. *M. vitrata* peaked one week after flower maximum, which was still one week before the larval peak of thrips. Before the damage by thrips through flower shedding became important, *M. vitrata* already had built up a moderate population.

Megalurothrips sjostedti. Both stages of thrips, larvae and adults, did not significantly react on treatments and densities did not show important variation. Although larval numbers dropped after DAP 63, adults kept a relatively high abundance feeding on flowers, which were still present at DAP 70, since the cowpea variety used was semi-determinate.

Second season (II/95)

Maruca vitrata. Neither abundance nor densities were of important variation among treatments. Already with the flower peak at DAP 49 (Fig. 3.12.), adult thrips migrated in from alternative host plant in high numbers. Before cowpea was sown, two different *Tephrosia* sp. carried thrips continuously, particularly adults that reacted strongly to early flower set in cowpea. Subsequently, flower numbers remained low and restrained *M. vitrata* from building up an important population, being masked by earlier and remarkable damages by thrips, especially larvae (DAP 56), to the same resources (Taylor 1967; Jackai & Singh 1991).

Megalurothrips sjostedti. *Senna* was least attractive for thrips larvae as *Imperata* was for adults (Fig. 3.12.). Since neither flower numbers (Fig. 2.16.) nor other recorded measures (e.g., planting density, missing plants, soil quality among treatments) could explain these patterns, this phenomenon was ascribed to particular characteristics of the respective mulch type. These might be olfactoric or visual stimuli, to the particular expression of which thrips responded. The control was similar to *Imperata* and neem mulch for larvae and to *Senna* and neem for adults, not indicating an effect of mulch in general. To clearly identify particular stimuli by mulch types was beyond the scope of this study and an analysis was not attempted. In general, the pest pressure from neighboring wild hosts (Fig. 7.13.) was strong and led to fast migration of adults into cowpea as soon as the first flowers appeared. Densities for larvae were recorded highest in the control at DAP 56 as a result of a remarkable drop of flower numbers on this sampling day and a peak in larval abundance.

Third season (I/96)

Maruca vitrata. The control together with *Imperata* mulch yielded the most larvae, but the control in parallel recorded significantly lowest flower numbers at the peak of DAP 49 (Chapter 2). Since the control as a no-mulch treatment and *Imperata* mulch, with its high lignin content a relatively resistant material to decomposition, were similar, a general mulch effect was excluded. In turn, *Senna* and neem mulch, in structure very similar and probably decomposing in a similar time period, resulted in corresponding preference by thrips. Stigter et al. (1994) found a decomposition of *Senna* of about 70-90% within 60 days. Due to the similar structure of neem, its leaves were expected to decompose in about the same time. This would have suggested an enrichment of the soil with effect on nutritive requirements for herbivorous insects like *M. vitrata* and eventually attracting them in relatively higher numbers. The contrary was the case (Fig. 3.13.), which did not confirm this alleged influence. However, the differences were not very large and were probably the response to other influences, which were not soilborne or plant inherent. In terms of densities, the control was significantly higher than neem mulch. This was the ratio of comparatively highest flower numbers in neem mulch and lower larval numbers than in all other treatments. This ratio showed that the higher abundance of *M. vitrata* in the control, in contrast with neem, was principally due to fewer available resources rather than a real treatment effect.

Megalurothrips sjostedti. Both stages, larvae and adults, did not reveal considerable variation. Fig. 3.13. indicated an earlier peak of larvae in the control of one week. Although mulch treatments recorded lower soil humidity (Fig. 2.17a.), they probably provided nutrients through increasing decomposition (Stigter et al. 1994) and thus delayed plant senescence (Sinclair & de Wit 1975, 1976; Summerfield et al. 1983; Wien & Summerfield 1984). Thrips, particularly larvae, which have high nutritional requirements for growth and molting (Mollema & Cole 1996), probably reacted to this slight shift in plant metabolism (Ananthakrishnan & Gopichandran 1993). Densities, too, did not suggest variation among treatments.

Fourth season (II/96)

Maruca vitrata. Very dry conditions during this season with a precipitation <100 mm resulted in small plants and very low flower set, which did not attract *M. vitrata.* Thrips adults occupied the few flowers right at the flowering peak producing high numbers of offspring, which reached their maximum one week later (DAP 63). This additional stress apparently further decreased the suitability of resources for *M. vitrata*. Some few larvae were found in different treatments on two consecutive DAPs but due to low values, no attempt was made to interpret this.

Megalurothrips sjostedti. Whereas adults did not result in differences among treatments larvae developed differently in the control than they did in mulch (Fig. 3.14.). Since the season was very dry (DAP 42 recorded the last rainfall in this season), and alternative host plants were

not diverse (Fig. 7.15.) nor did they carry an important population, adult migration into cowpea was limited. Larval numbers remained low in the control but developed considerable numbers under mulch with their maximum one week after the one of the control. In this particularly dry and warm season larvae obviously were protected under mulch while pupating in the soil litter (Lewis 1973); the emerging adults subsequently probably oviposited on the same plants, yielding these high numbers. Densities for larvae differed at least for the control and *Senna*, reflecting the low larval numbers in the control and high numbers in *Senna* rather than varying flower numbers. The effects between the control and mulch thus were confirmed.

Fifth season (I/97)

Maruca vitrata. Although no significant variation was found among treatments, neem seemed to have attracted more larvae than all other treatments. However, none of the measured data (e.g., flower numbers, thrips abundance, soil quality, soil humidity, plant size) indicated a related influence on larvae. This effect was regarded as unspecific. Densities also did not suggest important variation.

Megalurothrips sjostedti. Thrips larvae moved in similar profiles over time and peaked at the same time (Fig. 3.15.). Adult migration into cowpea was delayed by precipitation at the early flower peak of *Imperata* and neem. When rainfall was interrupted at DAP 56, migratory adults possibly found *Senna* more attractive because there were slightly more flowers during the two weeks. However, since the flower numbers had already dropped on the aging plants, oviposition did not exceed that of other treatments. Alternative host plants were scarce and *Tephrosia candida*, which was monitored, carried a low population, the migration from which was not expected to be important. This resulted, except for adults in *Senna*, in generally moderate thrips numbers. Densities for adults in *Senna* were not found to be more elevated and were attributed mainly to tendentiously more flowers and a thus higher total carrying capacity (Tamò et al. 1993b) in this treatment.

Conclusions

Four factors were identified that influenced populations of *M. vitrata* and *M. sjostedti*. These were NPK fertilizer, climate, alternative host plants in the vicinity of cowpea fields, and mulch. Mulch, on which this study was focused, demonstrated the least important effects and generally interacted with the other parameters. Only NPK fertilizer and host plants were found to explain regional variation as main effects. NPK application resulted in higher flower set and increased suitability in terms of nutritive requirements for both *M. vitrata* and *M. sjostedti*. If mulch was found to cause changes in population, mainly as organic matter itself and less frequently in combination with NPK, positive properties of chemical nutrient supply and beneficial mulch effects enhanced each other. In most cases, indirect effects were the reason due to

increase of flower numbers. Shelter and direct nutritive effects each appeared once. Some so-called unspecific cases were encountered, where the properties of one particular mulch type must have been the reason for pests' preference, e.g., visual or olfactoric stimuli. Since the other mulch types in the same cases did not lead to similar results, a general mulch impact on pests contrasting the control could not be confirmed.

Alternative host plants and climatic conditions turned out to strongly guide pest dynamics on the basis of available resources (flowers). Thrips were affected much more strongly than *M. vitrata*, which, in addition, depended on number and time of presence of thrips in flowers. Host plants were the principal reservoir for population build-up, from where often massive migration originated. Larvae of *M. vitrata* were found only once in higher numbers in an alternative host (*Dolichos africanus*). It was assumed that migration originated from plants that occurred outside the monitoring area of this study. If weather conditions were favorable for thrips, host plants represented a remarkable potential for migration, resulting in damaging invasion into cowpea fields.

Weather conditions for thrips consisted of two patterns, one being the total amount of rainfall per season and the second due to the timing of precipitation in relation to the flowering period of cowpea. Generally, high precipitation restrained thrips adults from important migration or killed them (Tamò, pers. comm.). When flowering coincided with rainfall, migration was delayed. Thus, positive effects on subsequent yields are likely. A delayed population build-up might limit the abundance of thrips because of decreasing resources on the aging plant. The masking effect of thrips on populations of *M. vitrata* was confirmed. When thrips' migration was delayed, *M. vitrata* larvae were more abundant in flowers given a minimum of required organs.

Application of chemical fertilizer and mulch proved to increase vigor of plants, producing more nodes and tendentiously more flowers (Chapter 2). In this chapter, a positive response of pests to increased availability of resources (flowers) as well as nutritive quality was demonstrated. The outcome is a fragile equilibrium between a higher carrying capacity (Tamò et al. 1993b) on the one hand and increased damage by larger populations on the other hand.

In line with the conclusions from Chapter 2, direct application of NPK fertilizer is not to be recommended. Mulch alone or in combination with chemical fertilizer suggested weak influence on plants in the same way as it appeared for pest populations. The underlying direct or indirect effects of mulch do not justify the high labor requirements. To achieve stronger effects in view of antagonists' populations, a long-term use might be envisaged, contributing to a generally higher vigor of plants. High thrips numbers towards the second rainy season considerably reduce the yield potential of cowpea. In view of economic yield, cowpea cultivation during late cropping seasons often implies uneconomic use of labor and seeds if efficient protection is not feasible.

4 Parasitism on different developmental stages of *Maruca vitrata* and *Megalurothrips sjostedti* in flowers and pods of cowpea vis-à-vis different soil covers (mulch) and two soil nutrient levels (NPK)

ABSTRACT Death rate analysis was used to assess mortalities of eggs and larvae of *Maruca vitrata* F. (Lepidoptera: Pyralidae) and larvae of *Megalurothrips sjostedti* Trybom (Thysanoptera: Thripidae). Egg parasitism of *M. vitrata* by *Trichogrammatoidea* sp. (Hymenoptera: Trichogrammatidae) was assessed while exposing carrier plants in the different treatments. Three braconid parasitoids, *Dolichogenidea* sp., *Phanerotoma leucobasis* Kriechbaumer, and *Braunsia kriegeri* Enderlein (Hymenoptera: Braconidae), represented the dominant species of a guild of parasitoids attacking the five instars of *M. vitrata*. *Ceranisus menes* Walker (Hymenoptera: Eulophidae) was the only parasitoid that caused mortalities to larvae of *M. sjostedti*, the efficiency of which was at very low levels. Five factors were isolated that explained variability in parasitization rates most appropriately: alternative host plants, qualitative properties of the cowpea plant (NPK), larval age, larval abundance, and physical aspects of refuge for antagonists (mulch). The presence of suitable alternative host plant communities in the vicinity of cowpea enhanced parasitoid activity, resulting in increased mortalities of pest larvae. Regional as well as seasonal distinctions in parasitism levels were mainly ascribed to presence or absence of alternative feeding and oviposition sites for antagonists. The change of metabolism in plants by NPK application exerted a positive impact on parasitoids via their host medium, the larvae of both pest species. When assessed over time, fertilizer influence was attributed to faster growth and aging of plants, with parasitoids' response shifting accordingly. A negative density-dependent mortality rate of larvae was proposed for *M. vitrata* and *M. sjostedti*. The increasing abundance of pest larvae was met by decreasing relative parasitization successes. Parasitization rates of *M. vitrata* were influenced by the proportion of early to late instars, which were targets of basically three different species with varying oviposition preferences. The overlap of two parasitoid species on early instars yielded comparatively higher mortalities than one species alone that was attached to late instars. Depending on the population age structure, mortalities differed considerably. Isolated cases, where parasitoids appeared to benefit from a shelter effect of mulch, gave rise to the conclusion that this secondary benefit did not make mulch an appropriate tool for pest control. Only in cases where the other, comparatively stronger influences, were absent, did influences of mulch become apparent.

Different methods exist for assessing parasitism (Simmonds 1948; van Driesche 1983; van Driesche & Bellows 1988; van Driesche et al. 1991), but not every method is appropriate to tackle mortality bound to parasitism. However, every approach is likely to bias results in various ways, as results can be regarded as estimators that always lack some information, eventually biasing the results (Simmonds 1948; Miller 1954; van Driesche & Girisco 1979; van Driesche

1983; Wolda 1988). Under the given conditions, which are discussed in Chapter 1, the death rate analysis proposed by van Driesche et al. (1991) was reckoned most appropriate.

Although a number of antagonists were found on cowpea pests (Fagade 1966; Taylor 1967; Kranz et al. 1979; Okeyo-Owuor et al. 1991; Arodokoun 1996; Tamò et al. 1997), research is still lacking evidence on their dominant role on key pests in cowpea like *M. vitrata* and *M. sjostedti* on the African continent. *M. vitrata* attracts a guild of parasitoids; *Dolichogenidea* sp., *Phanerotoma leucobasis* Kriechbaumer, *Braunsia kriegeri* Enderlein, *Pristomerus* sp. (Hymenoptera: Braconidae) and a tachinid fly (Diptera: Tachinidae Sturmiini) were those most frequently observed during this study, which cover all instars. *M. sjostedti* is attacked by a single species (*Ceranisus menes* Walker [Hymenoptera: Eulophidae]). Parasitism rates on *M. vitrata* were reported for a single parasitoid species with up to 60% in cowpea and over 90% in alternative host plants (Arodokoun 1996). Considering all parasitoid species of the guild together, the total mortality level increases with the number of different parasitoid species (Ehler 1985). The single parasitoid of *M. sjostedti* proved highly inefficient (Tamò et al. 1993a, 1997). As for the parasitoids of *M. vitrata*, the egg parasitoid *Trichogrammatoidea* sp. is polyphagous (Arodokoun 1996) as is noted for trichogrammatids in general (Strand 1986). Little is known of the braconid species and the extent to which they might be polyphagous like other braconid species is as yet not assessed (Tamò, Goergen, pers. comm.). *C. menes* occurs on different thrips species, among which *M. sjostedti* is probably not the most important (Saxena 1971; Antsiferova & Timraleev 1974; Siddappaji & Reddy 1974; Saxena 1981; Daniel et al. 1983; Chiu 1984; Caltagirone 1985; Tachikawa 1986; van Driesche et al. 1987; Murai 1988; Chang 1990; Hirose 1990; Tamò et al. 1993c).

Host plant environment in terms of diversity and source for alternative hosts (van Emden & Williams 1974; Levins & Wilson 1980; van Emden 1981; Risch et al. 1983; Powell 1986; van Emden 1990; Altieri et al. 1993; Way & Heong 1994; van Driesche & Bellows 1996), nutritional profiles of host organisms due to a change in metabolism in the host plant (Bentz et al. 1996), and mechanical properties of soil cover like mulch (Baldy & Stigter 1993) are proposed as greatly modifying parasitoids' reproductive and feeding conditions. Even simpler environments like intercropped cowpea were reported to increase parasitism on *M. vitrata* (Agboh-Noameshie 1990; Oghiakhe et al. 1991). Whereas beneficial effects of alternative host plants and changes in metabolism of the plant is basically agreed upon, the effects of mulch like color (IRRI 1974; Kranz et al. 1979; Cruz 1981), odor (Arthur 1962), shelter (Baldy & Stigter 1993), and increase of antagonist populations (Fukuoka 1978; Violic et al. 1982; Müller-Sämann & Kotschi 1997) on insects are still controversial. The extent to which these influences can be made responsible for differences in parasitism rates on *M. vitrata* and *M. sjostedti* is assessed in this study.

Materials and Methods

Parasitization in flowers

Parasitism on the flower thrips. Flowers were collected to obtain living larvae of *M. vitrata* and *M. sjostedti* for parasitization studies. One receptacle with gauze cover (16.5 x 11 x 8 cm [length x width x height]) was filled per treatment and brought to the laboratory. To allow eggs to hatch overnight, the flower material was searched thoroughly one day after collection for all stages of larvae of *M. sjostedti*. They were transferred into small plastic tubes (5.7 x 5.8 cm; 5.8 x 3.2 cm – diameter x height for two sizes), each containing 30 larvae, and sealed with two layers of Parafilm®, enclosing three drops of sugar solution (Tamò, unpublished, after Murai 1990, modified) to be fed on. Each tube was equipped with a small piece of filter paper and 25 µl of water, which was found suitable to satisfy the need for humidity of larval and pupal stages (Mollema & Cole 1996).

Rearing tubes were kept at 28.2°C (± 0.04) for about 10 days, when larvae reached the adult stage. The temperature was measured three times per day with a digital thermometer (precision not known). The thrips were separated thereafter by adults (dead, living), dead larvae, and hatched parasitoids (dead, living) for assessment of the parasitization rates:

$$\text{Parasitization rate} = \frac{\text{number of parasitized larvae}}{\text{number of adults (living/dead)} + \text{number of prasitized larvae}}$$

Larvae that were lost through premature mortality due to manipulation or other factors (e.g., fungi, which developed during the rearing process) were discarded from analysis. The parasitoid always was a parasitic wasp, tentatively identified as *Ceranisus menes* (Hymenoptera: Eulophidae) (Tamò et al. 1993c), a polyphagous larval endoparasitoid of different thrips species.

Parasitism on the pod borer. The same flower material that was searched for thrips was kept for another 3 to 4 days to allow for hatching of eggs of *M. vitrata*. Afterwards, all found larvae of *M. vitrata* were isolated and, ordered by each instar, transferred into plastic tubes (2.5 x 3.8 cm; 1.7 x 3.4 cm – diameter x height for two sizes) on artificial diet (Ochieng & Bungu 1983; Jackai & Raulston 1988). Each tube contained one larva (or pupa), was closed with cotton wool and was kept at the same climatic conditions as the thrips tubes. As their life cycle lasts longer (Vishakantaiah & Jagadeesh Babu 1980; Okeyo-Owuor & Ochieng 1981; Singh & Jackai 1988), *M. vitrata* larvae were kept three to four weeks, when each tube was controlled for a normal developed, living adult. Since the consumption of larvae increases with each instar during the rearing process (Taylor 1967) (five instars, prepupa, pupa [nymph]), and the amount of excrement increases as well, each larvae had to be transferred more than once to

another tube with fresh diet source during the entire rearing process. As each larvae reached its nymphal stage it was again assigned to a new tube without diet (2.5 x 3.8 cm – diameter x height), as they pause feeding (Taylor 1978). At the end of the rearing process, tubes were segregated by adults (moth) and parasitized larvae of *M. vitrata,* respectively, the latter not reaching the adult stage. Instead, the endoparasitoid that developed inside the larvae was isolated. Larvae that were lost through premature mortality due to manipulation or other factors (e.g., fungi) were discarded from analysis. The parasitoids found can be categorized into two groups, those parasitizing eggs and early instars (normally stage 1 to 3) and those parasitizing late instars (stages 4 and 5). The group of early attacking parasitoids consisted of *Phanerotoma leucobasis* Kriechbaumer (Hymenoptera: Braconidae), *Dolichogenidea* sp. (Hymenoptera: Braconidae), and *Trathala* sp. (Hymenoptera: Ichneumonidae). The parasitoids killing mainly late instar larvae were *Braunsia kriegeri* Enderlein (Hymenoptera: Braconidae), a tachinid fly (Diptera: Tachinidae Sturmiini), *Pristomerus* sp. (Hymenoptera: Braconidae), and *Aphanogmus* sp. (Hymenoptera: Ceraphronidae) (Goergen, pers. comm.). However, the limits between those two groups are somewhat permeable, as *P. leucobasis* and *Dolichogenidea* sp. in some cases were found hatching out of later instars and *B. kriegeri* was also observed to emerged out of earlier instars. When talking of attack or parasitization of defined instar ranges of larvae, the moment is considered when the parasitoid is ovipositing into its host. Later on, the parasitoid becomes effective by killing its host through developing offspring in the interior of the host larvae. The pest organism thereby leaves the system through mortality (van Driesche 1983). Apart from *P. leucobasis*, known as to be an egg-larval parasite (Taylor 1967; Arodokoun, pers. comm.), there is still no clear evidence of when exactly the different parasitoids attack their host medium. The early attacking parasitoids predominantly kill their hosts within the same instar range (one to three), whereas parasitoids emerging out of late instars possibly oviposit into early instars as well. Different times of appearance of offspring out of host larvae might be explained simply by different time for development within the host.

The relationship between parasitism rates and larval densities of *M. vitrata* and *M. sjostedti* was sought by combining larval numbers in flowers, flower numbers on representative plants, and plant numbers in plots to obtain a realistic estimate of the larval population per unit and related parasitization levels (Lux, Tamò, Schulthess, pers. comm.). The underlying subsamples for the estimator of absolute larval numbers per plot (treatment) were: larvae per flower (mean of 20 randomly collected flowers per plot), flowers per plant (mean of 10 randomly selected plants per plot), number of plants per plot, and relative mortality rates. The plant numbers per plot were calculated using the mean of all estimated plant numbers per plot of all regions and seasons and the theoretically expected plant number on known plot size, number of rows and number of plants per row. In fact, the estimator of plant numbers and the theoretical value were close together. They were both pooled and the mean was generated to gain higher accuracy. Parasitism rates were obtained by filling a given volume (one receptacle with gauze cover (16.5 x 11 x 8 cm – length x width x height) per plot with flowers. The iso-

lated larvae per volume of flowers were reared and investigated for parasitism. These different measures also served other purposes like population dynamics in flowers or physiological studies of plants and were described in more detail in the respective chapters. On the basis of these measures, larval densities were calculated (Lux, pers. comm.):

$$N = X * Y * Z$$

where

N = absolute larval numbers per plot
X = mean of larvae per flower from a subsample of 20 flowers per plot
Y = mean of flowers per plant from a subsample of 10 plants per plot
Z = [(mean of plant estimates per plot for each region and season) + (theoretical value of plants per plot on give plot size, number of rows and number of plants per row)]/2

All cases in which no larvae were collected in flower subsamples or no flowers were counted on plant subsamples, were discarded from calculation since these cases would have resulted in zero. The values for parasitism for the corresponding case were grouped into the calculated larval numbers to be displayed in a scatter plot for *M. vitrata* and *M. sjostedti*, respectively.

Parasitization of eggs of M. vitrata

At IITA, eggs of *M. vitrata* were exposed for studies of parasitization. Since the eggs (0.65 x 0.45 mm: Broadley 1977; Taylor 1978; 0.695 x 0.498 mm: Okeyo-Owuor & Ochieng 1981) are deposited on stems, leaves, shoot tips, peduncles, flower buds, and flowers (Taylor 1978) of the whole plant, their observation in the field is difficult (Taylor 1967). To overcome this situation, a “carrier medium” was used to observe the number of exposed and parasitized eggs more efficiently in the laboratory under the binocular. This approach partly follows the trap host method by van Driesche et al. (1991), where non-parasitized hosts (usually from laboratory colonies) are placed in the field for short intervals, after which they are recovered. Young cowpea shoots were grown in the greenhouse in small plastic vials (2.5 x 3.8 cm – diameter x height) on rock wool to be used as carrier. Before being transported to the field, the vial was closed tightly with Parafilm® to minimize waterloss. Healthy shoots with two secondary leaves were chosen for the weekly intervals of exposure. They were exposed for 24 hours in cages (47 x 45 x 58.5 cm – length x width x height) to a small population of female adults of *M. vitrata*, which were reared as part of the permanent population at IITA. Subsequently, the deposited eggs on the young shoots were counted in the laboratory under the binocular before they were brought to the fields. Two shoots were chosen per treatment and placed within the

line between cowpea plants, representing a central point of each treatment half. Then, 24 hours later, they were collected, brought to the laboratory, marked, and once more controlled for remaining eggs. For another 48 hours, the shoots were kept in an insect-free laboratory (28.2°C ± 0.04). All insects to be reared were kept in the same laboratory at the same temperature. After this period, most of the parasitized eggs could already be distinguished by a small black dot, indicating the successful parasitization by the endoparasitic wasp, *Trichogrammatoidea* sp. (Hymenoptera: Trichogrammatidae). Different batches of eggs were cut off the shoots (visually separated into non-parasitized and parasitized eggs) and assigned to petri dishes (8.6 x 1.5 cm/plastic; 5.2 x 1.4 cm/glass – diameter x height), for the time being remaining with their leaf basis. As first instar larvae emerged that were not parasitized, they were transferred into plastic tubes (5.7 x 5.8 cm; 5.8 x 3.2 cm – diameter x height for two sizes) on artificial diet (Ochieng & Bungu 1983; Jackai & Raulston 1988). They were reared up to the adult to exclude any event of parasitization. The other eggs, being parasitized, remained in the petri dishes, where the emergence of *Trichogrammatoidea* sp. was awaited. Sterile eggs, which turned to orange color, were kept apart. During the whole observation period they were never the targets of parasitism. They were not considered for analysis as their number remained low. This exposure of "carrier plants" was done in weekly intervals as well. The basic aim of this approach was to investigate if the searching behavior of the trichogrammatoid wasp could be influenced by the soil cover (mulch) obviously changing the habitat structure in combination with color stimuli exception (Ananthakrishnan & Gopichandran 1993). Any bias of nutritional effects that might have guided parasitism successes could entirely be excluded since all shoots originated from the same laboratory colony based on the same treatment.

Parasitization of M. vitrata in pods

As far as *M. vitrata* is concerned, the later larvae, which move from flowers to pods, are continually the target of antagonists. For studies on this issue, weekly samples on 10 plants per treatment were collected (the same day as all other exercises). At the time of pod formation, random numbers were used to select the plants, which were harvested entirely and marked thereafter with a colored ribbon. They were thus excluded from subsequent pod sampling so as not to bias results. They were not removed, as this would artificially thin the plant population with its implication for the phenology of neighboring plants and subsequent possible influence on insect populations. All pods of the 10 plants were assigned to one envelope (33.5 x 16.5 cm/ 13 g; 45 x 20.5 cm/ 25 g – length x width/ weight for two sizes). During the counting in the laboratory, the pods were systematically scrutinized for all stages of larvae of *M. vitrata*, and all pods that showed a borehole were opened. The same procedure was applied to larvae found in pods as for those found in flowers. Again they were segregated into living adults and parasitoids that emerged out of reared larvae.

Statistical analysis. Responses on parasitism are categorical data and were expressed in percentage ± standard error of the mean (SEM). Larval numbers as well as eggs of *M. vitrata* exposed on "carrier plants" were not analyzed using arcsine-transformed percentages. To take into consideration the differing quantities of larval and egg numbers obtained from the plant material, GENMOD in SAS was used to adjust for these different sample sizes. The separate raw data of larval and egg numbers on the one side and the numbers of larvae or eggs parasitized on the other were used. Thus, the parasitized quantities were weighed for the respective sample size (number of larvae). On the basis of the generalized linear models (GLIM) (Nelder & Wedderburn 1972; Liang & Zeger 1986; Dobson 1990; Diggle et al. 1994; Lipsitz et al. 1994), repeated measures were applied, accounting for the particular covariance structure of the data, which was assumed as to be autoregressive (Box 1954; Kenward 1987; Legendre 1993). Data were logit transformed using GENMOD, recognizing their binomial distribution. After the likelihood-ratio statistics (Chi-square), which was used to test for treatment effects, *a priori* chosen contrasts assisted in separating means. Since GENMOD (SAS) does not furnish appropriate output that could be used for presentation, GENSTAT was used additionally on the same model to obtain detransformed mean ratios with standard errors of the means. Larvae of *M. vitrata* were analyzed in total (all instars together) and separately grouped for early instar larvae (first to third instar) and late instars (fourth and fifth instar) since they are attacked by different parasitoids according to their developmental stage. A comparison of the three parasitoids *Dolichogenidea* sp., *P. leucobasis,* and *B. kriegeri* revealed results on their relative dominance among themselves. Other parasitoids were of minor importance and were not analyzed this way.

To distinguish seasonal and regional patterns, factorial analysis across time was preferred over repeated measures. Particularly distinct profiles within each season and between first and second rainy seasons did not allow proper comparisons on trends. Instead, seasons and regions were incorporated as additional factors. For comparisons between regions and between seasons within regions, replications were nested within region and season respectively to use a hierarchical error term (Korie, pers. comm.).

A *P*-value of 0.05 was generally used to judge significance, although higher levels were considered as marginal responses if reckoned important. The c^2-values were marked with one star (*) if $0.05 > P \geq 0.01$ and with two stars (**) if $P < 0.01$. All results that represent proportions, e.g., percentage, are followed by the corresponding sample size in brackets.

The exact description of experimental sites and the research design, auxiliary data like climate and soil properties, and a detailed description of the statistical approach were discussed completely in Chapter 1 and may assist in further understanding of the presentation that follows.

Results

Regional differences

NPK was not used at IITA. Hence, regional differences were tested in two steps. An overall comparison on the three regions did not consider NPK, leaving mulch as single treatment factor. The neem treatment at IITA was excluded as well, which was a special component for the on-station trials only. A second step compared the two on-farm regions Tokpa/Ayou and Lema, controlling for NPK.

All regions

Maruca vitrata

Parasitism in flowers. *M. vitrata* was attacked at significantly higher rates in Lema, with 18.7^{d}% mortality due to parasitism compared with much lower levels in Tokpa/Ayou (3.8^{d}) and at IITA (1.6^{d}) (c^2 = 604.3**). Tokpa/Ayou was also higher than IITA. Across regions seasons I/95, II/95, and II/96 showed equal results, being significantly superior to seasons I/97 and I/96; the latter had the lowest successes of parasitoids, which was significantly lower than for season I/97 (c^2 = 166.0**) (Table 4.1a.). First growing seasons (I/95, I/96, I/97) together were significantly lower compared with the late seasons (II/95, II/96). Early instar larvae (first to third instar) followed the same regional patterns as larvae in total, with 23.8^{d}% parasitism in Lema, 4.8^{d}% in Tokpa/Ayou, and significantly lowest with 1.4^{d}% at IITA (c^2 = 665.6**). Among seasons, no variation occurred between season I/95 and seasons II/95, I/96 and I/97 (Table 4.1a.). The latter three differed from each other (c^2 = 160.7**). Season II/96 displayed significantly the highest mortality rate. As for total larvae, early instars followed the pattern of higher mortality during late cropping seasons. Late instar larvae were attacked most strongly in Lema (10.4^{d}), which was significantly higher than in Tokpa/Ayou (2.7^{d}) and at IITA (1.7^{d}), but the latter two were not different (c^2 = 113.2**). Seasons I/95 and II/95 were equal, as were seasons II/96 and I/97 (c^2 = 83.5**) (Table 4.1a.). Season I/96 had significantly the lowest reduction due to parasitoids. Seasons I/95 and II/95 revealed higher attacks on late instar larvae than seasons II/96 and I/97.

Parasitism in pods. Mortality was significantly highest in Lema (16.9^{d}) compared with Tokpa/Ayou (5.0^{d}) and IITA (2.5^{d}) (c^2 = 26.2**). IITA and Tokpa/Ayou showed about the same levels. Seasons did not vary to a significant extent, although season I/96 seemed to be lowest whereas season I/97 yielded slightly higher parasitism rates than the other seasons (Table 4.1b.). Early instar larvae followed the same regional pattern, favoring Lema (24.7^{d}) sig-

nificantly over Tokpa/Ayou (12.9[d]) and IITA (3.5[d]) ($c^2 = 9.1^*$). Tokpa/Ayou and IITA did not differ. Too few numbers of early instar larvae were found in pods to allow analyses on seasons. However, analysis suggested a general mulch effect across regions, yielding very low mortality in *Imperata* mulch (6.2[d]%) compared with the control (21.5[d]) and *Senna* (21.8[d]), both of which were significant against *Imperata* ($c^2 = 7.0^*$). Late instar larvae followed the general regional patterns significantly favoring Lema (18.4[d]) compared with Tokpa/Ayou (4.0[d]) and IITA (2.0[d]), the latter two being close together ($c^2 = 24.6^{**}$). Seasonal variation was not important, although season II/95 seemed to record highest mortality. However, this lead was consumed by a high variability (Table 4.1b.). Seasons I/96 and II/96 remained relatively low. A marginal effect was uncovered in favor of mulch treatments *Senna* (7.8[d]) and *Imperata* (8.9[d]), both with higher mortality than the control (4.7[d]) ($P \geq 0.05$).

Megalurothrips sjostedti

Lema demonstrated significantly highest mortality (2.9[d]%) – superior to Tokpa/Ayou (1.1[d]) and IITA (0.3[d]). IITA also had significantly lower losses than Tokpa/Ayou due to parasitism ($c^2 = 448.9^{**}$). As for seasons across regions, I/97 and I/95 revealed highest parasitism rates not differing from each other ($c^2 = 686.8^{**}$) (Table 4.2a.). Together they significantly exceeded levels of the other seasons. Season II/95 displayed significantly the lowest attacks. All first rainy seasons together revealed significantly higher parasitization rates contrasting with the very low levels of second growing seasons. Parasitoids seemed to have been influenced differently by mulch types in Lema and Tokpa/Ayou. In Lema, the highest mortality occurred in *Senna* mulch, but in Tokpa/Ayou this was the treatment with the lowest rates (Table 4.2b.). The control in Tokpa/Ayou revealed maximum attacks. *Imperata* mulch resulted in lowest attraction for the parasitoid in Lema. The inverse relationship in the two regions for the control versus *Senna* and *Senna* versus *Imperata* produced a significant interaction ($c^2 = 15.9^{**}$).

On-farm regions

Maruca vitrata

Parasitism in flowers. In addition to the general regional effect favoring Lema, NPK application had an impact on parasitism in combination with mulch, which was different between the two regions (three-way interaction). When comparing Lema with Tokpa/Ayou, mortalities changed inversely between *Senna* mulch versus the control and *Imperata* ($c^2 = 6.3^*$) (Table 4.3.). Whereas parasitism was inferior in *Senna* for both NPK levels in Lema in comparison to the control and *Imperata*, the same pattern applied in Tokpa/Ayou for the non-fertilized plots only. As for fertilized treatments in Tokpa/Ayou, the effects were inverse, indicating highest mortalities for *Senna* with NPK. Mulch was not different across regions. A par-

tial NPK effect was observed insofar as NPK always resulted in increased parasitism in Lema. In Tokpa/Ayou this was true for *Senna* plots only. However, the control and *Imperata* did not follow this pattern but rather decreased slightly in combination with fertilizer. A simple effect resulted in the fact that plots without NPK were significantly different between mulch types across regions. *Senna* had lowest mortalities in both regions contrasting the control and *Imperata* ($c^2 = 8.6^{*}$) (Table 4.3.). Within fertilized treatments, this was not confirmed across regions. Early instar larvae showed, in addition to the regional effect, a marginal increase due to NPK fertilizer ($P \geq 0.05$). Parasitism rates could be increased by roughly 4 percentage points from 16.0^{d}% to 20.1^{d} having applied fertilizer. Late instar larvae increased by 1 percentage point from 6.4^{d}% in blank plots to 7.4^{d} when NPK was applied ($P \geq 0.05$).

Parasitism in pods. Parasitism yielded inverse results on mulch when combined with NPK. Mortality rates of total larvae decreased when fertilizer was applied for the control plots, but increased due to fertilizer for both mulch types across the two regions ($c^2 = 9.1^{*}$) (Table 4.4a.). Separated by simple effects the control was parasitized at a significantly higher rate than *Senna* and *Imperata* within non-fertilized plots ($c^2 = 8.8^{*}$). Mulch types did not vary significantly from each other. Within fertilized treatments *Senna* recorded significantly higher mortalities than the control but was not significantly different from *Imperata* ($c^2 = 6.1^{*}$) (Table 4.4a.). Early larvae followed a similar pattern on the interaction ($c^2 = 7.1^{*}$). The control without NPK was attacked most strongly, but no mortalities were found in mulch (Table 4.4b.). In turn, *Senna* displayed the highest mortalities compared with the control and *Imperata* when combined with fertilizer. Within non-fertilized plots, larvae in the control were attacked only, the mulch treatments remaining at zero mortality. This difference was significant ($c^2 = 9.5^{**}$). Within fertilized plots, the differences were not significant. However, the numbers of early larvae for the exercise were very low. Late larvae separately confirmed the general pattern of mulch due to NPK impact (Table 4.4c.). The control revealed higher mortalities without fertilizer but had lowest levels when NPK was applied ($c^2 = 6.3^{*}$). The only simple effect occurred within fertilized plots where the control remained at a significantly lower level than *Senna* and *Imperata* ($c^2 = 7.3^{*}$).

Megalurothrips sjostedti

When assessed for NPK effects larval mortality was significantly higher in fertilized plots ($c^2 = 116.5^{**}$) (Table 4.5.).

Seasonal differences within the same region

Tokpa/Ayou

Maruca vitrata

Parasitism in flowers. Total larval mortality was significantly lowest in season I/96 against all other seasons ($c^2 = 90.8^{**}$) (Table 4.6a.). Season II/95 was not different in parasitism levels from seasons I/95 and II/96, but II/96 yielded more parasitized larvae compared with season I/95. These three seasons were also superior to season I/97. Early instar larvae were attacked significantly more in season II/96 compared with all other seasons ($c^2 = 53.4^{**}$) (Table 4.6a.). Seasons I/95, II/95, and I/97 were close together in mortality rates. Season I/96 did not reveal differences compared with II/95 but was inferior in mortality to seasons I/95 and I/97. Assessment of late instar larvae described two seasonal clusters, seasons I/95, II/95, and II/96, and seasons I/96, and I/97; the clusters were not different within each other but the first cluster scored higher in mortality than the second one ($c^2 = 57.3^{**}$) (Table 4.6a.). There appeared also an interaction of mulch in combination with NPK. The control displayed slightly and *Senna* remarkably higher parasitism due to fertilizer application while the contrary happened for *Imperata* mulch, which dropped slightly under NPK impact ($c^2 = 8.7^{*}$) (Table 4.6b.).

Parasitism in pods. Mortality on total larvae did not vary in seasons. An effect among mulch types was found due to NPK application. The control without fertilizer had the highest attacks (9.8^{d}%) and *Imperata* the lowest (1.9^{d}); *Senna* was intermediate (3.4^{d}). In fertilized plots the control (2.4^{d}) suffered the lowest mortality whereas in turn *Senna* was targeted most often (7.7^{d}), leaving *Imperata* in between (4.5^{d}) ($c^2 = 6.4^{*}$). Early larvae were found in too few numbers to be considered separately. Adult larvae demonstrated no difference due to treatments or seasons.

Megalurothrips sjostedti

Parasitism rates changed differently in mulch treatments according to NPK application and between seasons. This three-way interaction was significant ($c^2 = 18.9^{**}$) (Table 4.7.). No attempt was made to formulate all mutual differences but the inherent main effects were looked into. Season II/95 was discarded from analysis since the very low level of parasitized larvae negatively influenced the model fit. Rounding to four digits after the decimal point for means still resulted in zero values, and they have therefore been treated as zero mortality. On the remaining seasons a significant variation was recognized ($c^2 = 119.3^{**}$). Seasons I/95 and I/96 did not differ significantly but both were superior to season I/97. These three seasons showed higher mortalities than season II/96.

Lema

Maruca vitrata

Parasitism in flowers. Season I/95 was discarded from analysis since very few larvae were found. With one exception application of NPK always increased the mortality rates for larvae ($c^2 = 25.0^{**}$). This exception was *Imperata* in season I/97, which dropped in levels after NPK application. Early larvae followed the same pattern for the NPK effect with the exception of *Imperata* in season I/97 ($c^2 = 21.4^{**}$) (Table 4.8.), but the differences between NPK levels were more accentuated. For late instars, NPK had no significant impact. A look at seasonal comparisons showed that season II/95 had the best results on parasitism and was significantly superior to seasons I/96, II/96 and I/97 ($c^2 = 37.4^{**}$) (Table 4.9.). Seasons II/96 and I/97 were close but had significantly more attacks than season I/96.

Parasitism in pods. For analysis of total larvae seasons I/95 and II/95 were discarded because of no parasitism events and season I/97 resulted in three parasitized larvae only. Hence, analysis was carried out using seasons I/96 and II/96. Results for seasons I/96 (overall parasitism 13.5^{d}%) and II/96 (14.3^{d}) did not suggest any differences. Numbers of parasitized larvae were generally low.

Megalurothrips sjostedti

Seasons I/95 and II/95 had to be discarded from analysis, the first not revealing any parasitized larvae and the second with few larvae only. A significant NPK effect was found across seasons ($c^2 = 604.3^{**}$) (Table 4.10.). NPK application always resulted in higher larval mortality. Comparisons among the remaining seasons indicated significantly higher parasitism in season I/97 in contrast to seasons I/96 and II/96, which were close together ($c^2 = 684.2^{**}$).

IITA

Maruca vitrata

Eggs. Exposure of carrier plants to investigate egg parasitism was started with season II/95. Except for *Senna* mulch in season I/97 a general seasonal effect was discovered (Table 4.11.). *Senna* mulch in season I/97 revealed comparatively high mortality rates and invalidated an overall higher mortality rate in seasons II/95 and I/96 compared with I/97, but the effect applied to the other treatments for this particular comparison. Season II/96 was least in parasitism rates ($c^2 = 111.7^{**}$). Across seasons the *Senna* treatments were significantly superior to *Imperata* mulch ($c^2 = 19.8^{**}$).

Parasitism in flowers. Seasons II/95, I/96, and II/96 had to be discarded from analysis since the few parasitized larvae did not allow proper comparisons. The remaining seasons, I/95 and I/97 with 1.4[d]% mortality and 1.8[d], respectively, did not reveal differences between each other and among treatments. This was worse for early and late instar larvae since they represent fractions of the whole larval numbers.

Parasitism in pods. Again, seasons II/95, I/96, and II/96 had to be dropped before analysis. The remaining two seasons together resulted in 240 larvae, out of which 10 were parasitized covering 48 observations. No differences occurred. The fractions of early and late instar larvae were too small for analysis.

Megalurothrips sjostedti

The two second rainy seasons II/95 and II/96 yielded few larvae with rare instances of parasitism and were not included in the analysis. The mortality rates were low in general and were based on relatively low numbers of parasitized larvae (Table 4.12.). Analyses tentatively uncovered a seasonal variation between seasons I/95, I/96, and I/97, indicating that mortality in season I/96 was significantly superior to scores found in I/97 ($c^2 = 11.0^{**}$).

Differences within seasons

Tokpa/Ayou

First season (I/95)

Maruca vitrata

Parasitism in flowers. Parasitism mainly occurred at DAPs 56 and 63. Larvae showed differences in trends for NPK on DAP ($c^2 = 4.3^{*}$) (Table 4.13a.). Mortality increased without NPK from DAP 56 to DAP 63, but dropped in fertilized plots from a comparatively higher level at DAP 56 to a quarter of its initial level at DAP 63.

Parasitoids in flowers. Three parasitoids were found attacking larvae of *M. vitrata* during DAPs 49, 56, and 63; these were *Dolichogenidea* sp., *P. leucobasis*, and *B. kriegeri*. Their dominance, i.e., the amount of larvae parasitized by each species, was found to be significantly different ($c^2 = 27.4^{**}$). *Dolichogenidea* sp. attacked 4.2[d]% of all larvae (24 parasitized larvae) and was not significantly different from *P. leucobasis*, which oviposited into 12.5[d]%. *B. kriegeri* showed clear dominance having killed 83.3[d]%, which was significantly more than the two other parasitoids.

Parasitism in pods. Too few parasitized larvae were found for analysis.

Megalurothrips sjostedti

No parasitism was found before DAP 56 and after DAP 63. Parasitism on thrips larvae followed similar patterns compared with *M. vitrata* larvae (Table 4.13b.). In treatments without NPK fertilizer mortalities were stable over the two sampling events DAP 56 and DAP 63 but, when fertilizer was used mortality dropped from 6.5^{d}% at DAP 56 to under 1 at DAP 63 ($c^2 = 13.9^{**}$).

Second season (II/95)

Maruca vitrata

Parasitism in flowers. The only mortality events occurred at DAP 63. Sixteen observations yielded 35 larvae, recording 14.7^{d}% parasitism in total. No treatment differences were found.

Parasitoids in flowers. Except for two *P. leucobasis*, the parasitoid in flowers was always *B. kriegeri*.

Parasitism in pods. Three larvae were found over three sampling weeks, none parasitized.

Megalurothrips sjostedti

Out of 4,698 larvae sampled during several weeks, only one was parasitized.

Third season (I/96)

Maruca vitrata

Parasitism in flowers. Six weeks of sampling resulted in 1,036 larvae, out of which five were parasitized. Analysis was not possible.

Parasitoids in flowers. The five larvae were parasitized by three *P. leucobasis* and two *B. kriegeri*.

Parasitism in pods. Of 76 larvae collected out of pods, only one was parasitized and that by *B. kriegeri*.

Megalurothrips sjostedti

Larvae varied among the control and *Imperata* versus *Senna* mulch differently when combined with NPK ($c^2 = 11.1^{**}$) (Table 4.14a.). Without fertilizer, mortality was about the

same in the control and *Senna*. Parasitism almost doubled when NPK was applied to the control and more than tripled in *Imperata*, but was lower in *Senna* due to fertilizer. Mortality rates decreased across treatments on a linear trend over time ($c^2 = 13.7^{[1]**}$) (Table 4.14b.). Whereas the drop from DAP 49 to DAP 56 was significant, mortality decreased only slightly between DAP 56 and DAP 63 and decreased again significantly towards DAP 70.

Fourth season (II/96)

Maruca vitrata

Parasitism in flowers. During two sampling events, 125 larvae were found in 32 observations, resulting in 15.5^{d}% mortality due to parasitism over all treatments. Differences were not suggested by analysis.

Parasitoids in flowers. Parasitoids behaved differently over the two sampling times. An interaction of parasitoid and DAP was suggested by analysis ($c^2 = 9.7^{**}$) (Table 4.15.). However, contrasts for means separation could not be estimated due to many non-parasitized events. The interaction obviously seems to explain the inverse behavior of *Dolichogenidea* sp. and *B. kriegeri* between DAP 56 and DAP 63. *Dolichogenidea* sp. was the dominant parasitoid at DAP 56, whereas for DAP 63 *P. leucobasis* had slightly more successes than *B. kriegeri*.

Parasitism in pods. Sampling resulted in 16 larvae in total, out of which 3 were parasitized by 1 *P. leucobasis* and two *B. kriegeri*.

Megalurothrips sjostedti

Sampling at DAP 56 and DAP 63 yielded 3,508 larvae in 32 observations. NPK application significantly favored parasitism ($c^2 = 3.9^{*}$). Mortality in plots without fertilizer recorded 0.7^{d}% at DAP 56 and 0.2^{d} at DAP 63 whereas this was 1.7^{d} and 0.4^{d}, respectively, when NPK was applied. The time main effect resulted in significantly higher levels at DAP 56, dropping towards DAP 63 ($c^2 = 10.4^{**}$).

Fifth season (I/97)

Maruca vitrata

Parasitism in flowers. Total mortalities for early instar larvae (6.1^{d}%) did not differ from those of late instar larvae (1.8^{d}). Considering all larval instars together, the control suffered significantly highest mortalities compared with *Senna* and *Imperata*, the latter yielding significantly higher parasitization rates than *Senna* ($c^2 = 19.7^{**}$) (Table 4.16.). Mortality peaked at DAP 56 for mulch treatments whereas the control scored highest at DAP 63. Para-

sitism appeared to be significantly more elevated at DAP 56 than DAP 63 ($c^2 = 10.3^{**}$). When investigated separately early instar larvae followed exactly the same patterns at a relatively higher mortality level. Within mulch types the control was significantly more attacked than *Senna* and did not show the other significant differences suggested for all larvae together. Late instar larvae displayed no significant variation among treatments and time points.

Parasitoids in flowers. Except for one *Dolichogenidea* sp., larvae were parasitized by *P. leucobasis* and *B. kriegeri* (Table 4.17.). The parasitoids' interaction with time was significant, indicating a dominance of *P. leucobasis* at DAP 49, which decreased over the following two weeks, while *B. kriegeri* grew in importance towards the later part of the season ($c^2 = 14.1^{**}$).

Parasitism in pods. Larval mortalities were separated on mulch treatments in combination with NPK. Parasitism occurred inversely between the control and *Senna* between the two NPK levels ($c^2 = 7.3^{*}$) (Table 4.18.). The control suffered highest mortalities when no fertilizer was applied, while at the same time *Senna* recorded no parasitism. Within fertilized treatments the control scored lowest but *Senna* revealed highest parasitism. *Imperata* was not influenced by NPK.

Parasitoids in pods. The 19 larvae that were parasitized yielded 11 *B. kriegeri*, 5 *P. leucobasis*, 2 tachinid flies, and 1 *Dolichogenidea* sp. The differences were not significant.

Megalurothrips sjostedti

Thrips larvae revealed different mortalities among mulch plots in combination with NPK ($c^2 = 604.3^{**}$) (Table 4.19.). The control increased little with NPK application whereas the increase in *Senna* mulch due to fertilizer was 4.5 times its low level without NPK. This same effect in *Senna* contrasted with no increase in *Imperata* due to fertilizer as well. Parasitism was generally higher in fertilized treatments ($c^2 = 7.6^{**}$).

Lema

First season (I/95)

Maruca vitrata

Parasitism in flowers. Parasitism events were found mainly at DAP 49 with the exception of two larvae parasitized by *B. kriegeri* at DAP 56. Analysis was carried out for DAP 49 only. The relatively low overall numbers of larvae resulted in a significant NPK*mulch interaction but failed to separate means using contrasts ($c^2 = 12.1^{**}$) (Table 4.20.). The control interacted with *Senna* on NPK levels and *Senna* also demonstrated an inverse mortality compared

with *Imperata* mulch. Within the non-fertilized plots, the control resulted in the most elevated mortality, but *Senna* did not reveal parasitization. Considering fertilized plots separately, *Senna* recorded the most parasitism incidences but *Imperata* did not show mortalities. Whereas the control and *Imperata* lost in parasitism efficiency due to NPK application, *Senna* gained when fertilizer was applied. Early instar larvae separately confirmed the patterns described for total larvae ($c^2 = 8.2^*$). Late instar larvae did not reveal significant variation by treatments.

Parasitoids in flowers. Out of the parasitized larvae hatched 14 *B. kriegeri*, 7 *P. leucobasis*, 1 tachinid fly, and 1 *Perilampus* sp., the latter known as a hyperparasitoid of several parasitoids on lepidopteran species (Goergen, pers. comm.).

Parasitism in pods. During four sampling weeks four larvae were found in total and no parasitism was recorded.

Megalurothrips sjostedti

Three weekly sampling events yielded 315 larvae with no mortality instance.

Second season (II/95)

Maruca vitrata

Parasitism in flowers. Total larvae varied among mulch treatments in combination with NPK fertilizer ($c^2 = 7.8^*$). The control showed a significant inverse mortality compared with *Imperata* when NPK was applied (Table 4.21a.). The relationship between *Senna* and *Imperata* showed the same patterns but this interaction was marginal. Within blank plots *Imperata* was on the highest level, while with NPK the control as well as *Senna* together were more strongly parasitized than *Imperata*. Application of fertilizer generally increased mortality rates in the control and *Senna* mulch but slightly reduced parasitism in *Imperata*. Early instar larvae followed the same pattern except for *Imperata* mulch, where mortalities also increased through fertilizer application (Table 4.21b.). Significant interaction occurred between the control versus *Senna* and *Imperata* ($c^2 = 7.4^*$). The control changed from the lowest parasitism level without NPK to the highest scores through use of fertilizer, obviously contrasting both mulch types. Late instar larvae differed marginally on the NPK*mulch interaction ($P \geq 0.5$) (Table 4.21c.). Whereas the control and *Imperata* had reduced parasitism levels in fertilized plots, *Senna* increased considerably. *Imperata* recorded highest mortality rates within non-fertilized plots while *Senna* scored highest within fertilized treatments.

Parasitoids in flowers. Parasitoids' oviposition behavior was found to differ between mulch treatments ($c^2 = 26.7^{**}$) (Table 4.22a.). *B. kriegeri* showed distinct patterns from those of *Dolichogenidea* sp. and *P. leucobasis* that differed from the control with each mulch type. Whereas *B. kriegeri* was more attracted to mulch plots, the other two parasitoids displayed a preference for the control. Across treatments sampling time uncovered a significant trend be-

tween DAPs 49 and 56 ($c^2 = 8.6^{*}$) (Table 4.22b.). Whereas *Dolichogenidea* sp. and *P. leucobasis* reduced oviposition events between the two sampling weeks, *B. kriegeri* increased its oviposition rate. However, the number of larvae parasitized in total at DAP 56 dropped remarkably. At DAP 63, one single larvae was parasitized by *B. kriegeri* but this was not included in the analysis.

Parasitism in pods. During three weekly sampling events five larvae were collected one of which parasitized by a tachinid fly.

Megalurothrips sjostedti

Five sampling weeks yielded 2,603 larvae, out of which five were parasitized.

Third season (I/96)

Maruca vitrata

Parasitism in flowers. Investigation of larval instars revealed significant variation of mortalities among the different stages ($c^2 = 133.7^{**}$). The second instar (29.6^{d}% [539]) resulted in significantly highest mortalities than all other stages. Instars one (14.4^{d} [278]), three (10.6^{d} [375]), and four (7.9^{d} [201]) did not differ significantly, but those three were also superior to the fifth instar (2.6^{d} [301]). The values in rectangular brackets are overall larval numbers on which parasitism was calculated. The means of early instar larvae (first to third) were also significantly higher than the ones for late instars (fourth and fifth). All larvae considered together showed a significant NPK effect, indicating generally higher mortality rates in fertilized plots ($c^2 = 10.7^{**}$) (Table 4.23a.).

Among the different mulch treatments parasitism also changed in levels due to NPK application ($c^2 = 8.2^{*}$). This was significant between the control and *Senna* versus *Imperata* mulch. If no NPK was applied, mortalities in the control were significantly highest compared with *Senna* and *Imperata,* the latter remaining lowest within non-fertilized plots ($c^2 = 13.5^{**}$, simple effect). Within fertilized plots *Senna* had significantly lower mortality rates than the control and *Imperata,* the later two recording about the same values ($c^2 = 14.1^{**}$, simple effects). A marginal mulch effect was suggested on profiles ($P \geq 0.05$) (Table 4.23b.). The control had higher scores at DAP 42 than *Senna* and *Imperata,* peaked at DAP 49, which was also the highest level, and dropped under the rates for mulch at DAP 56. *Senna* started with the lowest mortalities and increased slightly from DAP 49 to DAP 56. *Imperata* constantly increased in parasitism rates during the three weeks when parasitized larvae were found in the fields.

Early instar larvae (n = 50, trials = 1,192, events = 240) followed exactly the same patterns, being significant at the NPK main effect ($c^2 = 10.7^{**}$), the NPK*mulch interaction ($c^2 = 9.3^{**}$), and the respective simple effects per NPK level. Their mortality rates were more ele-

vated on the particular factor combinations. Parasitism rates steadily rose from 12.2[d]% [128] at DAP 42 passing DAP 49 with 20.4[d] [855] to their maximum at DAP 56 (25.1[d] [209]), the last sampling day when parasitized larvae were found. Late instar larvae (n = 45, trials = 502, events = 29) did not vary significantly on treatments. Their mortality levels dropped from 28.8[d]% [18] at DAP 42 to 3.0[d] [249] at DAP 49, and increased again to 7.6[d] [235] at DAP 56.

Parasitoids in flowers. During the whole season the three parasitoids *Dolichogenidea* sp., *P. leucobasis,* and *B. kriegeri* were recorded exclusively. Parasitism occurred from DAP 42 until DAP 56; one *B. kriegeri* was found at DAP 63 only. In general, *Dolichogenidea* sp. appeared at the lowest level, which was significantly less than *P. leucobasis* and *B. kriegeri*. *P. leucobasis* was also significantly superior to *B. kriegeri* ($c^2 = 147.2^{**}$) (Table 4.24.). A mortality trend was revealed for the parasitoids indicating a significant difference over time between *P. leucobasis* and *B. kriegeri* on the second order polynomial ($c^2 = 19.0^{[q]**}$). *P. leucobasis* increased to its maximum oviposition at DAP 49 and dropped afterwards. *B. kriegeri* decreased by about 50% towards DAP 49 and doubled its initial parasitism rate afterwards.

Parasitism in pods. During DAPs 56 and 63, 148 larvae were collected. No significant variability in parasitism events was encountered due to treatments; the overall mortality was 14.3[d]%. At DAP 49 single organisms of *Dolichogenidea* sp., *P. leucobasis,* and *B. kriegeri* were found and DAP 63 yielded one *P. leucobasis* plus three *B. kriegeri*. DAP 56 separately yielded 18 parasitized larvae, 1 of which was killed by *Dolichogenidea* sp., 3 by *P. leucobasis,* and 14 by *B. kriegeri.*

Megalurothrips sjostedti

Larvae could be separated on NPK levels demonstrating a generally higher parasitization rate in fertilized treatments ($c^2 = 7.1^{**}$) (Table 4.25.). Parasitism in mulch also interacted with fertilizer. The relationship between *Senna* mulch versus the control and *Imperata* was significant ($c^2 = 10.9^{**}$). The increase due to fertilizer application was strongest in *Senna*. *Imperata* attracted the least parasitism over both NPK levels. Within non-fertilized plots mulch did not show significant variation but within fertilized plots *Imperata* had significantly lower mortality rates than the control and *Senna* ($c^2 = 14.0^{**}$).

Fourth season (II/96)

Maruca vitrata

Parasitism in flowers. During this season, comparatively high larval numbers permitted investigation of single instars (Table 4.26.). In general, second instar larvae suffered the highest mortalities followed by first instars without significant difference. All the other stages were significantly different in parasitism rates among each other ($c^2 = 144.3^{**}$). Except for the first two instars, mortality decreased the higher the instar level became. When grouped, early instar

larvae were parasitized more heavily than late instars. This effect did not apply entirely for *Senna,* for which a comparison of fourth and fifth instars showed an inverse effect. Larval instars were attacked differently among the mulch types. A comparison of the control with *Senna* mulch for second versus third instars revealed the same patterns as for the fourth versus fifth instars. All the other instars had significantly different patterns. The comparison of *Senna* with *Imperata* resulted in significant differences in patterns between second and third instars versus fourth and fifth instars ($c^2 = 31.7^{**}$). Generally, early instar larvae met the lowest attacks in *Senna* mulch, and in the same treatments mortality rates in turn were most elevated for late instar larvae.

All instars together resulted in significantly higher parasitism rates when fertilizer was applied ($c^2 = 31.9^{**}$) (Table 4.27a.). An impact of mulch was observed in general ($c^2 = 25.4^{**}$). The control suffered significantly highest losses due to parasitism compared with mulch treatments *Senna* and *Imperata*. No significant variation occurred between mulch treatments. When split into simple effects no considerable variation occurred within non-fertilized plots. Fertilized plots looked at separately for the three mulch levels were significantly distinct ($c^2 = 23.7^{**}$). The control again was superior, followed by *Imperata* and *Senna*. The only events of parasitism were encountered at DAPs 49 and 56. Mortality rates of 35.1^{d}% [1,272] at DAP 49 dropped significantly to 15.9^{d} [207] one week later ($c^2 = 37.5^{**}$). Early instar larvae separately marked similar patterns for the general NPK main effect, being higher in fertilized plots ($c^2 = 21.9^{**}$) (Table 4.27b.). Among mulch types ($c^2 = 34.6^{**}$) *Senna* suffered significantly the lowest mortalities. The control was close to *Imperata*. Within non-fertilized plots (simple effects), the control was significantly superior to *Senna* but not to *Imperata*. Within fertilized plots the control revealed about the same parasitism levels as *Imperata,* but both were significantly higher than *Senna* ($c^2 = 25.6^{**}$). NPK did not have significant effects on late instars. *Senna* was significantly different from *Imperata* mulch ($c^2 = 7.0^{*}$) (Table 4.27c.). *Senna* recorded the highest mortalities and *Imperata* remained on the lower end leaving the control in between.

Parasitoids in flowers. Parasitoids behaved differently on NPK levels ($c^2 = 172.1^{**}$) (Table 4.28.). *P. leucobasis* generally was significantly dominant over *Dolichogenidea* sp. and *B. kriegeri*, which was significantly lower than *Dolichogenidea* sp. This effect came principally from within fertilized plots ($c^2 = 198.3^{**}$, simple effects). Comparing non-fertilized plots separately, *B. kriegeri* and *Dolichogenidea* sp. did not differ from each other but were inferior in mortality rates to *P. leucobasis* ($c^2 = 44.2^{**}$). The effect of fertilizer was different for parasitoids, leading to significantly increased oviposition rates of *Dolichogenidea* sp. and *P. leucobasis,* but causing a drop for *B. kriegeri* ($c^2 = 19.2^{**}$).

Parasitism in pods. During three sampling weeks 125 larvae were obtained, which was too small a number to carry out a full analysis on factors. However, the comparison between instars confirmed the patterns already found in flowers. The group of early instars (first instars, 60.0^{d} [10]; second, 50.0^{d} [4]; third, 16.0^{d} [25]) was attacked significantly more severely than the later instars (fourth, 7.1^{d} [14]; fifth, 9.7^{d} [72]) ($c^2 = 15.8^{**}$). However, these results are

based on few larvae per instar. The parasitoids hatching out of parasitized larvae were three *Dolichogenidea* sp., six *P. leucobasis*, six *B. kriegeri*, one tachinid fly and three *Aphanogmus* sp.

Megalurothrips sjostedti

Fertilizer application resulted in significantly more accentuated parasitism than the blank plots ($c^2 = 30.5^{**}$) (Table 4.29.). As for mulch effects larval mortalities were significantly lower in the control compared with both mulch treatments ($c^2 = 28.5^{**}$). The two mulches *Senna* and *Imperata* were marginally different from each other, slightly favoring *Senna* in terms of parasitism levels ($P \geq 0.05$). Simple effects within non-fertilized plots recorded no significant variation, but within plots where NPK was applied all treatments differed among each other ($c^2 = 23.7^{**}$).

Fifth season (I/97)

Maruca vitrata

Parasitism in flowers. Larvae were found to be the target of changing parasitism over time. When comparing early instar larvae with late instars, an inverse trend could be discovered ($c^2 = 83.2^{**}$) (Table 4.30.). First instars were never the target of parasitoids. The remaining early instars (second and third) peaked in mortalities at DAP 49 and dropped thereafter to low levels at the end. Second instars were not the object of oviposition during DAPs 56 and 63, but with increase of larval numbers parasitism occurred again. Mortalities of late instars tendentiously increased during the season, being more accentuated for fifth instars. Total larvae were distinct between mulches at the two NPK levels (Table 4.31a.). This was significant between *Imperata* versus the control and *Senna* ($c^2 = 10.6^{**}$). Through this inverse mortality rates the control revealed lowest levels without NPK, whereas *Imperata* suffered significantly highest losses compared with the control and *Senna* ($c^2 = 13.0^{**}$, simple effects). In turn, *Imperata* remained at lowest mortality levels with NPK, and *Senna* attracted parasitoids most strongly. However, these differences within fertilized plots were not significant. Parasitism appeared to change differently over time among NPK levels ($c^2 = 13.2^{**}$) (Table 4.31b.). Plots without NPK showed lower mortality levels than their corresponding fertilizer treatments at DAP 42, but increased more strongly during one week peaking higher at DAP 49 than fertilized plots. Both levels set back together at DAP 56, when fertilized plots again started increasing to higher parasitism at the end of the season at DAP 70. This happened in parallel with overall increasing larval numbers.

Parasitoids in flowers. As far as variation among parasitoids is concerned, *P. leucobasis* and *B. kriegeri* were not significantly different. Both were significantly more dominant across

time than *Dolichogenidea* sp. ($c^2 = 56.9^{**}$) (Table 4.32.). The three parasitoids behaved distinctly over time (DAP) ($c^2 = 59.3^{**}$). However, no clear trends were obtained on the first and second order polynomials. *Dolichogenidea* sp. was ovipositing in low numbers and did not appear after two weeks. *P. leucobasis* was dominant during the first two sampling weeks (DAPs 42, 49) and peaked at DAP 49. After a setback at DAP 63, oviposition rates increased again in the last week. *B. kriegeri* appeared with rates slightly below 20^{d}% and steeply increased their attacks at DAP 63, being dominant during the last two weeks. Sampling at DAP 56 yielded one *P. leucobasis* and one *B. kriegeri* and had to be discarded from analysis. At DAP 49 several other parasitoids were recorded: five *Perilampus* sp., a hyperparasitoid of several parasitoids on lepidopteran species (Goergen, pers. comm.), one tachinid fly, and one *Trathala* sp.

Parasitism in pods. Three sampling weeks yielded 3 *B. kriegeri* out of 22 larvae in total.

Megalurothrips sjostedti

Parasitism developed on a linear trend between profiles of NPK levels ($c^2 = 16.5^{[l]**}$) (Table 4.33.). Comparatively high levels of parasitism were recorded during this season. Profiles for non-fertilized plots rose from low levels at DAP 42 to their mortality peak at DAP 56 decreasing thereafter. Within NPK plots mortality began sixfold higher than in blank plots at DAP 42. Mortality remained constant in the week following DAP 42, but then doubled, rising to a sharp peak at DAP 56. This pattern corresponded to the one for blank plots. At DAP 70, mortalities for fertilized plots dropped below the levels for plots without NPK. The common peak of both NPK levels coincided with a remarkable setback in larval numbers, which were sampled on this day. Between DAP 42 and DAP 63 fertilized plots suffered higher oviposition events by parasitoids than the ones without NPK.

IITA

First season (I/95)

Maruca vitrata

Parasitism in flowers. During the whole sampling period 7 parasitized larvae were isolated out of 102. Four were from neem treatments, two from *Imperata,* and one in the control. Parasitism occurred in samples from DAPs 49 and 56.

Parasitoids in flowers. Except for one, which was parasitized by *P. leucobasis*, the other larvae died from oviposition of *B. kriegeri*.

Parasitism in pods. The 112 larvae gathered yielded two organisms being parasitized by *B. kriegeri* at DAP 63.

Megalurothrips sjostedti

Six larvae were found to be parasitized at DAP 56 out of the 1,226 that were sampled during the whole season.

Second season (II/95)

Maruca vitrata

Eggs. An investigation of profiles of mulch type revealed variations on trend (c^2 = 42.5**) (Table 4.34.). The control was significantly different on the second order polynomial from *Senna* and neem. Whereas mortality in the control decreased steadily during three weeks *Senna* started on a slightly higher level, dropped to zero at DAP 70, and rose again one week later to a higher level than the control. Mortality in the neem mulch was found to be similar to *Senna*, starting with 100%, decreasing steeply at DAP 70, and rising to the level of the control. *Imperata* decreased constantly as well, at a relatively low rate, and was thus found to differ significantly from neem on a linear trend. The mulch main effect did not hold in general but was valid for the comparison between the control and *Imperata*, favoring the control with its significantly higher parasitism (c^2 = 16.1**). The generally highest oviposition successes by *Trichogrammatoidea* were recorded at DAP 63 on generally low egg numbers on the carrier plants.

Parasitism in flowers. Some 22 larvae were obtained in total, out of which two were parasitized, one by *P. leucobasis* at DAP 56 and one after oviposition by *B. kriegeri* sampled at DAP 70.

Parasitism in pods. Three weeks of sampling yielded three larvae, of which none was parasitized.

Megalurothrips sjostedti

A total of 2,988 larvae was obtained during five weeks of sampling, but only two larvae were attacked, one at DAP 49 and the other at DAP 63.

Third season (I/96)

Maruca vitrata

Eggs. Profiles of mulch types showed differences in trends over time ($c^2 = 115.5^{**}$) (Table 4.35.). The control was significantly different from *Senna* on a linear trend and from neem on a quadratic trend over time. The control decreased from its highest mortality level at DAP 28 to DAP 56, where it reached almost zero. In turn, *Senna* started with less than 20.0^{d}% and rose to a peak at DAP 42. Neem started close to the values for the control and peaked one week later. At DAP 42 it scored almost zero, but parasitism then sharply increased to a second peak before falling back to zero. *Imperata* closely followed the shape of the profile for neem until DAP 42, from where it dropped to zero. The mulch main effect suggested by analysis did not apply in general but was true for the comparison of neem versus *Imperata,* the latter always scoring less ($c^2 = 21.7^{**}$).

Parasitism in flowers. Six weeks of sampling revealed 991 larvae in total; at DAP 56 three of these were found to be parasitized, one by *P. leucobasis* and two by *B. kriegeri*.

Parasitism in pods. Some 173 larvae were collected in three weeks of sampling, but no parasitism occurred.

Megalurothrips sjostedti

While sampling over six weeks 4,185 larvae were obtained, 29 of which died due to parasitism. Since they were dispersed over the whole period, events of attack were too few to be tested among factors.

Fourth season (II/96)

Maruca vitrata

Eggs. A total of 786 eggs was exposed during six weeks from DAP 35 until DAP 70, but only 29 were parasitized. Tentatively DAP 56 and DAP 70 were analyzed separately. Not enough eggs could be obtained for DAP 63. DAP 56 indicated 14.3^{d}% [49] parasitism for *Imperata* and 4.5^{d} [44] for neem; the control and *Senna* were not targets of oviposition by *Trichogrammatoidea*. *Imperata* was suggested to be significantly superior to the control and *Senna* ($c^2 = 14.9^{**}$). As for DAP 70, *Senna* recorded 1.4^{d}% [71] mortality and neem 25.0^{d} [32]; the control and *Imperata* were not targets of attacks. Neem was found to be significantly different from the control ($c^2 = 26.1^{**}$).

Parasitism in flowers. Four weeks' sampling yielded 29 larvae, one of which was parasitized by *P. leucobasis* when collected at DAP 63.

Parasitism in pods. Two larvae were obtained in total, being collected at DAP 56. No parasitism occurred.

Megalurothrips sjostedti

The 2,967 larvae gathered during sampling over four weeks revealed one parasitized organism at DAP 56.

Fifth season (I/97)

Maruca vitrata

Eggs. In total 2,147 eggs were exposed, with 303 events of parasitism. Except for 40 parasitized eggs this principally happened during DAPs 42-56. The remaining 40 oviposition events occurred at DAP 63 until DAP 77, based on 1,223 larvae collected during these last three weeks. Since these events were accumulated on only a few occasions, an analysis model could not be fit to this part of the data. However, during these three later weeks 5 larvae were parasitized in the control, 13 in *Senna*, 10 in *Imperata,* and 12 in the neem mulch. During DAPs 42-56, egg mortalities appeared to be significantly different between the control and *Senna* the latter being superior in oviposition successes to the control ($c^2 = 52.6^{**}$) (Table 4.36.). A difference in trends over time was obtained between the control versus *Imperata* and neem ($c^2 = 23.3^{[q]**}$). Mortalities in the control decreased towards DAP 49 and rose thereafter. *Imperata* demonstrated constant rates during the first two weeks, slightly dropping at DAP 56. Neem started with higher levels than the control and *Imperata* and remained constant after a decrease of almost 30%. *Senna* showed a similar trend to the control on a higher level and inversely different starting and end points.

Parasitism in flowers. From DAP 49 until DAP 63 in total 881 larvae were collected, out of which 16 were parasitized by 2 *Dolichogenidea* sp. (DAP 49), 3 *P. leucobasis* (DAP 49) and 11 *B. kriegeri* (DAP 49-63). The respective mortalities for the control (0.7^d% [197]), *Senna* (1.9^d [253]), *Imperata* (2.9^d [271]), and neem (1.7^d [160]) did not vary significantly. Mortalities increased over time from 1.0^d [575] at DAP 49 to 1.7^d [230] at DAP 56 and significantly rose towards DAP 63 to 9.5^d [76] ($c^2 = 10.6^{**}$).

Parasitism in pods. Larvae from pods could be obtained at DAP 56 and DAP 63 only and yielded 128 organisms. Parasitism was recorded by one *P. leucobasis* (DAP 56) and seven *B. kriegeri*. Analysis was not possible.

Megalurothrips sjostedti

Three weeks of sampling revealed in total 4,520 larvae in 36 observations, among which nine were found parasitized. No effects were detected due to treatments or time. The overall

parasitization rate recorded 0.2[d]% only. Parasitism changed over time from 0.1[d] [1,647] at DAP 49 to 0.4[d] [1,123] at DAP 56, and to 0.2[d] [1,750] at DAP 63.

Discussion

Regional differences

All regions

Maruca vitrata

Parasitism in flowers. Parasitism was most elevated in Lema compared with Tokpa/Ayou and IITA. Lema also revealed significantly higher larval abundance, the number of which represented a more favorable source for parasitoids (Arodokoun 1996). The number of plant species serving as alternative hosts for *M. vitrata* and its natural enemies was higher than in both other regions (Appendix) suggesting an increase in both pest and antagonists based on increased diversity of habitat (van Emden & Williams 1974; Levins & Wilson 1980; van Emden 1981; Risch et al. 1983; van Emden 1990; Way & Heong 1994). Tokpa/Ayou also showed a higher potential of alternative host plants, in which antagonist populations were developing. At the IITA station, which is intensively cultivated, potential wild host plants rarely reached the stage of flowering, and, if present, were of low abundance. The only exceptions were *Tephrosia candida* and *Cajanus cajan*, both being cultivated as intercrops.

Neither *M. vitrata* nor its antagonists met propitious conditions for an important population build-up. The vicinity of the capital Cotonou posed another disadvantage in view of undisturbed habitat. Parasitism levels were higher in late seasons compared with early ones since *M. vitrata* accumulates during the season (Tamò et al. 1993b) and parasitoids subsequently. Otieno et al. (1983) observed that highest parasitization instances occurred towards the end of the cycle of the cultivated host, which might furnish supplemental explanation. Additionally, many host plants start flowering towards the second half of the year, creating rich alternative resources for pests and antagonists (Arodokoun 1996). Little is known of the behavior of the parasitoids of *M. vitrata,* nor is the extent to which they might be polyphagous like other braconid species (Tamò, Goergen, pers. comm.). Whereas populations of *M. vitrata* late in the year are generally expected to be larger (Arodokoun, 1996), their abundance in cowpea flowers is reduced due to increased damage by flower thrips (Taylor 1964; Singh & van Emden 1979; van de Klashorst & Tamò 1995). Parasitoid populations are expected to be larger as well following the increased abundance of prey (Hawkins & Goeden 1984). Season I/95 showed

higher mortality rates than seasons I/96 and I/97 despite being a first cropping season. Overall most larvae were counted in this season, suggesting an earlier population build-up of *M. vitrata* followed by its antagonists.

Parasitism in pods. Given that Lema recorded the highest diversity in perennial alternative host plants favoring a more stable and abundant population of antagonists of *M. vitrata* (Andow & Risch 1987; Arodokoun 1996), significantly lowest pod numbers probably resulted in significantly highest parasitism rates in this region. Attracted by relatively higher larval numbers of *M. vitrata* in cowpea flowers, parasitoids during their search on the plant probably encountered more frequently the few larvae in generally fewer pods compared with the other regions. Although not significant, a slightly higher parasitization rate was found in mulch than in the control. Tendentiously, mulch might have represented a better shelter for parasitoids during the hottest time of the day, a possibility that is also given credence by Baldy & Stigter (1993). Since *M. vitrata* larvae, being active nocturnally (Taylor 1978), are known to descend from the plants during daytime, a more frequent encounter between the parasitoid hiding under mulch and the larvae of *M. vitrata* probably caused higher mortality levels (Lux, Neuenschwander, pers. comm.).

Megalurothrips sjostedti

Parasitism was very low in all regions. Tamò et al. (1997) stated a total mean of below 1% of parasitized larvae under field conditions. *Ceranisus* is indeed very polyphagous (Saxena 1971; Siddappaji & Reddy 1974; Saxena 1981; Daniel et al. 1983; Chiu 1984; Caltagirone 1985; Tachikawa 1986; van Driesche et al. 1987; Murai 1988; Chang 1990; Hirose 1990), and *M. sjostedti* in cowpea seems not to be of primary importance. Antsiferova & Timraleev (1974) found parasitism levels of *C. menes* of up to 17% on the pea thrips, and Tamò et al. (1997) used artificial no-choice conditions to reach 15% on *M. sjostedti*. Lema revealed comparatively higher mortality rates due to parasitoids' oviposition. This was strongly related to a higher diversity of alternative host plants in the vicinity of the cowpea fields. For plants with more than 10 thrips larvae per flower (the highest category), Lema recorded six species of high importance, whereas at IITA two were recorded. Tokpa/Ayou did not reach a similar larval abundance in alternative host plants (Appendix). In the category of medium importance, Lema recorded nine species whereas Tokpa/Ayou and IITA revealed three species each. When including all species where thrips larvae were found, Lema again recorded a considerably more diverse habitat with 32 species, contrasting Tokpa/Ayou with 18 and IITA with 17 species. Biodiversity and stability of habitat may have positive implications for the activity of natural enemies (van Emden & Williams 1974; Levins & Wilson 1980; Risch et al. 1983; van Emden 1990), leading to higher larval mortalities.

Early seasons recorded higher parasitization rates than late ones and season II/95 showed lowest mortality among seasons. It is suggested that parasitism rates do not increase as fast as the population of thrips grows (Fig. 4.1.). Since all late seasons revealed significantly higher

thrips numbers, the proportion of parasitized larvae decreased as abundance rose. Season II/95, which had the most elevated thrips counts in flowers, in turn demonstrated significantly lowest parasitization levels. The interaction of mulch with region indicated higher mortalities in *Senna* mulch in Lema, whereas the same mulch treatment in Tokpa/Ayou yielded lowest mortalities. This happened together with highest larval numbers in *Senna* mulch in Lema and lowest in Tokpa/Ayou in the same treatment. This might be explained by larval numbers, which developed faster than the parasitoid population did.

On-farm regions

Maruca vitrata

Parasitism in flowers. A positive effect on parasitism rates followed the fertilizer application in cowpea in Lema. Slightly higher flower numbers had attracted scarcely more *M. vitrata*. Parasitization rates were higher, too. It is likely that the better suitability of larvae feeding on better nourished plants resulted in higher oviposition of parasitoids as was stated by Bentz et al. (1996) for whitefly and its parasitoid. In Tokpa/Ayou the variation between non-fertilized and fertilized plots in terms of larval mortality followed the same pattern but was limited to *Senna* mulch. The fact that it occurred in *Senna* is possibly attributable to the lower number of larvae in both *Senna* treatments, favoring parasitism on lower larval numbers; the parasitoids' preference may also stem from the fertilizer influence on larvae of *M. vitrata*. *M. vitrata* was also found to be less severely attacked in *Senna* mulch in non-fertilized treatments. This might be explained by slightly higher flower numbers and subsequently more larval numbers, which were more difficult to control by parasitoids.

Parasitism in pods. An inverse effect occurred among mulch treatments based on NPK levels. Mulch in combination with fertilizer attracted more parasitoids, whereas the control without NPK showed higher mortality. In the case of mulch, the combination of shelter for parasitoids under mulch (Baldy & Stigter 1993) with the nutritional advantage of applied fertilizer might be proposed as leading to more oviposition on present larvae (Bentz et al. 1996). When receiving fertilizer, the control yielded 1.5 times more larvae per 20 flowers than the non-fertilized control. This possibly reduced the number of parasitized larvae relatively. However, the slight difference in larval numbers was not of importance in mulch among NPK levels and was assumed to be of minor influence given the favorable conditions for parasitoids under mulch with fertilizer. Nevertheless, the underlying fertilizer effect was considered stronger than the shelter effect by mulch.

In assessments of non-fertilized plots separately, the control revealed higher mortalities than both mulch plots, the two of which counted slightly fewer larvae than the control. Although a positive mulch effect due to shelter and higher parasitism rates on comparatively lower larval numbers would be expected, the opposite happened. It is possible that on overall

low numbers in this case the chance of parasitoids to encounter larvae at all due to higher numbers in the control was increased. Once inside the pods larvae are better protected against parasitoids, additionally reducing the success rate of the parasitoid. However, no evidence could be found from literature. A comparison among fertilized treatments pointed to higher parasitization successes in *Senna* than in the control. A synergistic effect was believed to account for this difference. *Senna* in combination with fertilizer increased nutritional suitability of larvae (Bentz et al. 1996) and offered shelter through soil cover (Baldy & Stigter 1993), but counted fewer larvae than the control, which could have led to relatively higher parasitization rates. Early larvae were obtained in very low numbers. Within non-fertilized plots, the control yielded parasitized larvae only. As explained for total larvae, the chances of encountering larvae at all probably were higher in the control with 19 larvae in total compared with 7 and 12 larvae in *Senna* and *Imperata* treatments, respectively. Results for late larvae were similar to those for total larvae, suggesting the generally prevailing synergistic effect in the same way.

Megalurothrips sjostedti

Despite slightly higher larval numbers in fertilized plots, parasitization rates were higher, too. The positive nutritional effect for larvae followed by increased preference for oviposition (Bentz et al. 1996) probably best explain the increase in fertilized treatments. However, the observed increase by roughly 100% was biologically not important since even in fertilized treatments the parasitization levels remained below 3% (Table 4.5.).

Seasonal differences within the same region

Tokpa/Ayou

Maruca vitrata

Parasitism in flowers. Seasons I/96 and I/97 recorded lowest parasitization levels compared with the other seasons. At the same time larval abundance was highest in these two seasons. It is suggested that these high larval numbers reduced parasitism events in a negative way. Both seasons received the highest amount of rainfall and counted in parallel highest flower numbers. These basic requirements attracted *M. vitrata*, but parasitoids did not follow with their population build-up. As Way & Heong (1994) stated, increasing biodiversity can be one-sided, leading to higher attacks of pests. Since both seasons were early cropping seasons, the parasitoid population probably could not follow the development of the pest population. Parasitoid occurrence is thought to be highest towards the end of the crop under cultivation (Otieno et al. 1983). Thus, season II/96 showed best results on parasitism. Rainfall was lowest

in this season and larval numbers were by far lower than in seasons I/96 and I/97. Whereas *M. vitrata* developed a larger population during the early growing seasons, damages in late seasons due to thrips suppressed an important population. Greathead (1987) notes that the appearance of parasitoids is more delayed in temporary agroecosystems like cowpea, and in the present study this coincided with lower larval numbers. Lower pest numbers are likely to increase relative parasitization rates (Fig. 4.1.). A NPK*mulch interaction was suggested by analysis, indicating that parasitism on late instars in *Senna* treatments were distinct from the rates in the control and *Imperata* (Table 4.6b.). Without NPK *Senna* remained at lowest levels, whereas after fertilizer application its rates were double those in *Imperata* mulch and still higher than those in the control. *Senna* without NPK recorded more flowers than with NPK, probably strongly dispersing larvae within the plot. Apart from that, the differences among NPK levels were small remaining below 1% in change except for *Senna*.

Parasitism in pods. The control and *Imperata* mulch showed an interaction on both NPK levels. Without fertilizer, the control recorded higher parasitism events than *Imperata*, whereas the latter was superior to the control when fertilizer was used. In both comparisons, the control counted more larvae than *Imperata*, possibly due to more pods and slightly higher flower numbers. Without NPK, very few larvae were collected over five seasons (below 100), leading to a higher chance of encountering larvae at all in the control. *Imperata* possibly yielded too few larvae, which hardly were discovered by the parasitoids. In turn, fertilized treatments carried about double the larval numbers than blank plots did. The control had higher pod numbers, which probably dispersed larvae more than in *Imperata*, which had lower larval numbers but also fewer pods.

Megalurothrips sjostedti

Season II/95 was discarded from analysis because it recorded almost no parasitism, although thrips numbers were highest in this season. *Centrosema pubescens* and *Cajanus cajan*, monitored as alternative host plants in the neighborhood, hosted very few thrips numbers until the onset of flowers in cowpea. The abundance peak for adults occurred very late in cowpea. Antagonists rely on wild host plants as an alternative source (van Emden & Williams 1974; Powell 1986). The alternative hosts were present during this season, but low thrips numbers in these wild hosts were probably the reason why parasitoids did not appear in important numbers. Season II/96 recorded lowest parasitism rates while the second largest larval numbers were obtained in this season. Although alternative host plants were present, *C. pubescens* and *Cassia hirsuta* with moderate and *C. cajan* with higher thrips abundance in flowers, parasitism by *Ceranisus menes* remained low in cowpea. Its polyphagous behavior (Antsiferova & Timraleev 1974; Daniel et al. 1983; Chang 1990) and the limited parasitism rates even under no-choice conditions in the laboratory found by Tamò et al. (1997) seem to confirm that increased larval numbers do not lead to improved parasitism successes (Fig. 4.1.). Highest parasitism

rates in season I/96 in parallel with lowest thrips abundance seems to affirm the patterns of relatively higher parasitism levels on fewer available larvae.

Lema

Maruca vitrata

Parasitism in flowers. Season I/95 had to be discarded since few larvae were obtained. No potential host plant was found in the close neighborhood, and the surrounding vegetation was therefore not considered a favorable resource for antagonists (van Emden 1990; Altieri et al. 1993; van Driesche & Bellows 1996). The remaining seasons demonstrated a positive influence of NPK on parasitism levels, which is thought to stem principally from the better suitability of the host (Bentz et al. 1996), the larvae of *M. vitrata*. More larvae were also obtained in all fertilized plots. The driving force was possibly the improved nutritional quality, which increased parasitism despite rising larval numbers. Investigated separately, late instars displayed highest parasitism rates during season II/95 and lowest in season I/96. Larval numbers collected in flowers remained lowest in season II/95, but reached highest numbers during season I/96. This may be explained by the parasitoids' delay in instances (Greathead 1987), not immediately following an increase in larval numbers of *M. vitrata* by higher parasitism rates. This seems to be likely since season I/96 was an early season. In season I/96 the alternative host plant environment was particularly poor (Fig. 7.9.). The lack of diverse habitat did not exert a beneficial effect of antagonists (Levins & Wilson 1980; Risch et al. 1983) and resulted in low mortality among larvae of *M. vitrata*.

Parasitism in pods. Seasons I/95, II/95, and I/97 were excluded from analysis since they yielded few larvae only, with rare events of parasitism. Very few pods per plant were counted in the same three seasons, particularly in seasons I/95 and II/95. The pods in these seasons were few in number and very small in size, being mostly too small for late larvae to bore into.

Megalurothrips sjostedti

Seasons I/95 and II/95 were discarded from analysis since no or rare parasitization events were observed. The two seasons also counted lower flower numbers than the other three. Season I/95 was also very poor in alternative host plants, and together with lowest flower numbers in cowpea no important thrips population was built up that could have attracted the polyphagous parasitoid (Antsiferova & Timraleev 1974; Daniel et al. 1983; Chang 1990). Lack of natural vegetation was not favorable for the parasitoid to get installed either (Powell 1986; van Emden 1990; Altieri et al. 1993).

Season II/95 counted more flowers than I/95, resulting in more thrips larvae, and exhibited a more diverse alternative host plant environment where high thrips numbers were counted

in parallel. Although these conditions were expected to attract the parasitoid, parasitism rates were very low. This was ascribed to either better feeding and oviposition sources on which the polyphagous parasitoid could prey or the low total population of this antagonist. Across the remaining seasons (I/96, II/96, I/97) fertilized treatments always favored parasitism and doubled on average although larval numbers were higher in these plots, too. Fertilized plots may have increased numbers of parasitoids attracted by higher suitability of the food source (Bentz et al. 1996). Among the three seasons, II/96 recorded by far the lowest mortality rates, whereas season I/97 reached levels close to 8%. Season II/96, being a late cropping season, had accumulated a high number of thrips on a considerable number of wild host plants in the vicinity of cowpea (Fig. 7.10.). High abundance of thrips larvae, which possibly reduced relative parasitism rates together with a suggested distribution of the antagonist that was found by van Emden (1981) and Speight (1983), might be the reason for larval mortality rates of below 1% in this season. Season I/97 counted most larvae, which were found in highest numbers of flowers in cowpea, accompanied by a moderate diversity of alternative host plants close to the cowpea plots. Thrips levels remained moderate in these host plants. It is conceivable that an existing population of *C. menes* was attracted by high thrips numbers and relatively high flower numbers in cowpea while also relying on wild hosts around cowpea plots. Since only *Tephrosia bracteolata, T. platycarpa,* and *Lonchocarpus sericeus* were flowering (Fig. 7.11.), distribution among too many host plants was not to be expected (van Emden 1981; Speight 1983).

IITA

Maruca vitrata

Eggs. Since carrier plants were used as medium for eggs coming from the same laboratory colony, effects linked to plants and their metabolism can be excluded entirely as the driving force behind differences in suitability of the host, the egg. Season II/96 remained lowest in egg mortalities. In parallel, abundance of *M. vitrata* generally was low due to very dry conditions with rainfall less than 100 mm during the season (Table 2.6.). *Trichogrammatoidea* sp. is polyphagous (Arodokoun 1996), as noted for trichogrammatids in general (Strand 1986), and its fecundity depends among other factors on the availability of the host (Bai & Smith 1993; Manickavasagam et al. 1994). The prevailing dry conditions were not favorable for an important population build-up of *M. vitrata*, which therefore was not available in high numbers for its host. It cannot be estimated to what extent other hosts were more numerous, keeping *Trichogrammatoidea* sp. away from the eggs exposed in cowpea. However, since its relative oviposition successes possibly depended on total numbers of available eggs in a negative relation, these seasonal comparisons are of limited value. The numbers of eggs that could be exposed in the fields depended uniquely on the oviposition rate of *M. vitrata* adults in the laboratory to which the carrier plants were offered before exposure in the plots. Availability of eggs

on cowpea plants grown in the fields in each season might not correspond at all with the number of eggs obtained artificially in the laboratory. Against the background of probably less relative parasitism with increasing egg numbers, different numbers of exposed eggs among seasons are likely to bias results. Across seasons, eggs exposed in *Imperata* mulch recorded lowest parasitization rates – being significantly below those in *Senna* mulch. Total egg numbers exposed in both treatments were similar and a believed improved shelter effect (Baldy & Stigter 1993) under this slowly decaying mulch did not result in increased mortality of eggs. Also, numbers of *M. vitrata* larvae were not different, excluding effects caused by availability of eggs. It was possibly a specific effect of *Imperata* on stimuli such as surface structure, color, or olfactory particularities that led to these results (Altieri et al. 1978; Wien & Summerfield 1984; Ananthakrishnan & Gopichandran 1993; Baldy & Stigter 1993). Although plants were more developed in *Imperata* treatments than in *Senna*, a hiding effect of the exposed carrier plants in *Imperata* could not be argued with. Neem treatments, the plants of which were only slightly smaller, resulted in highest parasitization rates.

Parasitism in flowers and pods. Parasitization rates remained very low and during seasons II/95, I/96, and II/96 parasitization events were rare. Although precipitation varied considerably among seasons (Table 2.6.), numbers of *M. vitrata* did not follow these patterns significantly nor did mortalities change. This can probably be ascribed to the proportion of disturbed habitat close to the capital. Antagonists rely on a diversity of natural habitat (Levins & Wilson 1980; Risch et al. 1983; Powell 1986; van Emden 1990).

Megalurothrips sjostedti

As was the case for larvae of *M. vitrata*, very few parasitization events were recorded in all seasons. Although statistical analysis tentatively revealed variation between seasons I/96 and I/97, these differences were small and biologically irrelevant.

Differences within seasons

Tokpa/Ayou

First season (I/95)

Maruca vitrata

Parasitism in flowers, parasitoids in flowers, and parasitism in pods. Whereas parasitism levels in the non-fertilized treatments rose between DAP 56 and DAP 63, they fell in the fertilized plots. This happened in parallel with falling flower numbers (Fig. 2.5.) and larval

numbers (Fig. 3.1.), which followed the same patterns among NPK levels. The peak flower and larval numbers in fertilized plots occurred one week earlier and were higher than the non-fertilized treatments. Higher and earlier flowering was possibly the result of a NPK effect, which attracted larvae earlier and in higher numbers supposedly resulting in similar preferences by the parasitoids. The higher parasitism rates occurred possibly due to better suitability of the host after NPK application (Bentz et al. 1996), the decrease probably together with a faster senescence of the plants in these plots (Sinclair & de Wit 1975, 1976; Summerfield et al. 1978; Wien & Summerfield 1984). While reducing their search in older, less suitable plants in fertilized plots, parasitoids may have switched to non-fertilized plots where larval numbers did not drop and flowers were about to peak (DAP 63). These signs of suitability might have attracted parasitoids, resulting in slightly higher parasitism levels. However, the ratio between the three parasitoids (*Dolichogenidea* sp. *P. leucobasis*, *B. kriegeri*) developed towards *B. kriegeri* from DAP 56 to DAP 63, which is assumed to be a parasitoid related to late instars of *M. vitrata* (Arodokoun 1996; Tamò, pers. comm.). From DAP 49 on pods started to develop and became the target of late instars, which migrated to pods to finish their life cycle (Taylor 1978). This may explain decreasing larval numbers in senescing plants in fertilized plots and a shift of the exclusively found *B. kriegeri* towards pods at DAP 63 following late instars. Parasitization levels in flowers therefore remained low. *B. kriegeri* was the dominant parasitoid due to the advanced DAPs (56, 63) when a high proportion of late instars is expected to prevail. Pods did not offer valuable data on parasitism, yielding few parasitized larvae only.

Megalurothrips sjostedti

Patterns for *M. sjostedti* were similar to those for *M. vitrata*, suggesting similar reactions on suitability of the host induced by faster plant senescence in fertilized treatments. Since developing thrips larvae remain in flowers and descend to the soil only for pupation (Rösingh 1980; Mollema & Cole 1996), the parasitoid remains attracted to the flowers, too. An almost doubling abundance of thrips larvae was met probably through higher parasitoid numbers, which increased their incidence towards the end of the cycle of cultivated crops (Otieno et al. 1983). According to Greathead (1987), parasitoid populations are generally delayed in temporary agroecosystems. The diversity of alternative host plants in the vicinity of cowpea remained very poor and therefore was not a strong attractant for the parasitoid to migrate out of cowpea.

Second season (II/95)

Maruca vitrata

Parasitism in flowers, parasitoids in flowers, and parasitism in pods. Few larvae were encountered in this season in flowers, with the low number of parasitized larvae resulting

in misleadingly high parasitization rates. The sample size was too small to separate treatment effects. Only *B. kriegeri* hatched out of attacked larvae related to the late DAP (63) when mostly late instars were expected (Taylor 1978). Pods yielded no parasitized larvae.

Megalurothrips sjostedti

Although high thrips numbers were collected in cowpea flowers, only one was parasitized by *C. menes*. The thrips population seemed to have developed mainly in cowpea itself since their numbers in neighboring alternative host plants remained low and increased in parallel to first thrips collections in cowpea (Fig. 7.3.). This environment was considered not favorable as a source for antagonists (van Emden & Williams 1974; van Emden 1990; van Driesche & Bellows 1996). Parasitism in the alternative host plants *Centrosema pubescens* and *Cajanus cajan* were not observed, indicating a de facto absence of the parasitoid.

Third season (I/96)

Maruca vitrata

Parasitism in flowers, parasitoids in flowers, and parasitism in pods. Although relatively high larval numbers were collected in flowers, the very rare events of parasitism did not allow analysis. Only *C. pubescens* was present in the neighborhood, which did not reveal an attractive environment for parasitoid population build-up. The ratio of early to late instars was 1.5, possibly accounting for three *P. leucobasis* to two *B. kriegeri*; *P. leucobasis* emerges principally from early larvae (Arodokoun 1996; Tamò, pers. comm.).

Megalurothrips sjostedti

In the control and *Imperata* mulch parasitism rates increased due to NPK application, as distinct from almost no change in *Senna*, which decreased slightly. The increase in the control and *Imperata* mulch were ascribed to a NPK effect on the larvae, which in turn were preferred by the parasitoid (Bentz et al. 1996). The stable parasitism rates in *Senna* compared with both NPK levels could not be explained and were possibly due to a specific effect of *Senna* mulch. A general decline in parasitism levels occurred between DAPs 49 and 70. A first significant decrease happened in parallel with an 80% increase of the larval population accompanied by a slight decline in flower numbers thereby raising the density per flower. This growth in larval population possibly exceeded the development of the parasitoid, resulting in decreasing parasitization rates (Fig. 4.1.). Another significant decline in parasitization was recorded together with a sharp drop in larval numbers and also flower numbers. This was probably the point when the plant had senesced considerably and became less suitable for thrips, which migrated away from cowpea. Parasitoids possibly moved as well following its host.

Fourth season (II/96)

Maruca vitrata

Parasitism in flowers, parasitoids in flowers, and parasitism in pods. Very few larvae of *M. vitrata* were collected in this season. Thrips accumulated remarkably, especially adults (Fig. 3.4.), migrating from neighboring alternative host plants, which had relatively high numbers (> 10 adults per flower) (Fig. 7.5.). This led to high flower shedding through thrips damage, which probably suppressed the population of *M. vitrata*. This phenomenon is referred to as a masking effect by Jackai & Singh (1991). The relatively low larval numbers were possibly controlled more efficiently by the parasitoid, which found alternative sources (Powell 1986; van Emden 1990; Altieri et al. 1993), mainly *C. cajan* and *C. pubescens,* in the vicinity of cowpea. Therefore, relatively high parasitization rates were recorded. Between DAPs 56 and 63 the incidences by *Dolichogenidea* sp. decreased since this parasitoid basically attacked first and, to a much lower extent, second instars (Table 4.37.), which decrease in numbers towards the end of the season. *P. leucobasis* and *B. kriegeri* increased in numbers towards DAP 63. *P. leucobasis* was slightly more dominant than *B. kriegeri. P. leucobasis* attacked principally the second and third instars while *B. kriegeri* concentrated on fourth and fifth instars (Table 4.37.), which would have suggested a higher proportion of *B. kriegeri,* considering the late DAP. Flowering in this seasons peaked with a slight delay at DAP 56 and maximums of *M. vitrata* were subsequently recorded at DAP 63. It is likely that the proportion of early instars (first, second, third) at the peak was still high, favoring *P. leucobasis* over *B. kriegeri*, but the proportion of very early instars (first, second) was already low, explaining the drop to no parasitism by *Dolichogenidea* sp. at DAP 63. Pods yielded few larvae with rare parasitism successes, which reached almost 20% parasitism due to the low numbers.

Megalurothrips sjostedti

The slightly elevated mortality in NPK plots was ascribed to a nutritional effect on larvae, which probably increased the preference for these larvae by the parasitoid (Bentz et al. 1996). Larval abundance was slightly lower in fertilized plots and could have improved the number of successes by the parasitoid on a relative basis. Parasitism rates decreased from DAP 56 to DAP 63, which may be explained by the senescence of the plant (Wien & Tayo 1979; Wien & Summerfield 1984) where flower numbers decreased by this time. Parasitoids possibly switched back to alternative host plants, which also showed sufficient thrips numbers (Fig. 7.5.) in a more diverse habitat on which adults of natural enemies rely for pollen and humidity (Powell 1986; van Emden 1990; Altieri et al. 1993). However, the difference between NPK levels as well as the decline over time was too small to be of biological importance.

Fifth season (I/97)

Maruca vitrata

Parasitism in flowers, parasitoids in flowers, and parasitism in pods. Against the expectation of finding more parasitized larvae under mulch treatments due to favorable shelter conditions for parasitoids (Baldy & Stigter 1993), an increased mortality in the control was observed. More larvae were counted in the control but fewer flowers were recorded, leading to increased larval densities. As van Emden (1981) and Speight (1983) suggested, many plants or plant species can lead to a distribution of parasitoids. It is thus conceivable that more flowers, as counted in the mulch plots, have a similar effect. In turn, higher larval densities on the basis of fewer flowers could increase parasitoid successes. Parasitism rates in the control were also higher at DAP 49 while decreasing later on, whereas the mortality peak in mulch was delayed by one week, particularly in *Senna*. This coincides with higher larval numbers but lower flower counts in similar patterns, which became less distinct over time. Additionally, mortality decreased in general from DAP 56 to DAP 63 when at the same time larval numbers dropped sharply (Fig. 3.5.) and also flower production declined (Fig. 2.9.). This very likely indicated an overall reduced suitability of the plant for pests and antagonists ascribed to the progressive senescence of cowpea, which normally is induced by the seed filling period (Wien & Tayo 1979; Summerfield et al. 1978; Wien & Summerfield 1984). The decreasing parasitism rates by *P. leucobasis* in parallel to increasing rates by *B. kriegeri* show the shift in age of the population of *M. vitrata* between DAPs 49 and 63. Since *P. leucobasis* principally attacked second and third instars (Table 4.37.), its proportion of parasitized larvae decreased from 90% to 25% during the three weeks. Parasitism by *B. kriegeri* appeared the first time at DAP 56 and increased one week later as more late instars were to be expected. Instars four and five were the principal targets of attacks by *B. kriegeri* (Table 4.37.).

The interaction between NPK and the control versus *Senna* in pods could not be satisfactorily explained by the better suitability of larvae for parasitoids when feeding on fertilized plants nor could a shelter effect of mulch be assumed in general. Larvae in the control in non-fertilized treatments probably were more attacked as the larval numbers in both mulch treatments were very low and an encounter by the parasitoid was limited by low chance. After fertilizer application larval mortalities in *Senna* probably increased due to a higher oviposition preference by parasitoids on well-nourished larvae (Bentz et al. 1996). Mortalities in the control decreased despite an expected higher preference of nitrogen-nourished larvae, possibly because larval numbers were higher than in all other treatments reducing the proportion of successes. In congruence with findings that *B. kriegeri* causes highest mortalities on late instars, their expected dominance was confirmed by the fact that late instars especially bore into pods (Jerath 1968; Taylor 1978). *P. leucobasis* and *Dolichogenidea* sp. emerged much less frequently since their preference is biased towards early instars.

Megalurothrips sjostedti

Higher mortality was recorded in fertilized plots in general, which was assumed to stem from the positive nutritive influence on larvae and consequently better suitability for the parasitoid (Bentz et al. 1996). Larval abundance in the control was always higher than in both mulch treatments, therefore reducing the proportion of successes given the low efficiency of the parasitoid (Tamò, pers. comm.). However, these differences were of no biological importance.

Lema

First season (I/95)

Maruca vitrata

Parasitism in flowers, parasitoids in flowers, and parasitism in pods. DAP 49 was the only sampling event out of four weeks where more than five larvae could be isolated from flowers. However, their numbers were still too small to draw sound conclusions. Flowering was very short and was at its decline after DAP 42 (Fig. 2.10.). On this basis parasitism might have occurred rather by chance than by treatment preferences. The alternative host plant environment was particularly poor (Fig. 7.7.) mainly due to burning during the long dry season. Thus, a stable antagonist population could not develop in the vicinity of cowpea. Natural vegetation, in addition to the cultivated plant, serves as resource for alternative hosts and prey (van Emden & Williams 1974; van Emden 1990). Natural vegetation is also a source of pollen and humidity, which are necessary for adults of antagonists (Powell 1986; Altieri et al. 1993). The fact that mainly *B. kriegeri* and to a lesser extent *P. leucobasis* hatched indicated that the proportion of late instars predominated at this time. During four sampling weeks almost no larvae were obtained from pods, resulting in no parasitism.

Megalurothrips sjostedti

No parasitism was recorded on overall low larval numbers. The absence of potential alternative host plants (Fig. 7.7.) probably could not attract the parasitoid to the area in which cowpea was planted since no alternative resources for feeding and prey were available (van Emden 1990; Altieri et al. 1993).

Second season (II/95)

Maruca vitrata

Parasitism in flowers, parasitoids in flowers, and parasitism in pods. Mortalities on total larvae were reversed in *Imperata* mulch between early instars and late instars, which responded differently on NPK application. Whereas early instars showed increased mortalities in *Imperata* combined with fertilizer, a slight decrease was observed for late instars. However, effects on mortalities of late instars were not significant. NPK application generally led to higher parasitism levels in early instars, where the improved nutritional basis for larvae strongly attracted parasitoids (Bentz et al. 1996). Differences in mortality rates among NPK levels in the control were remarkable, in contrast to a moderate increase in mulch. Low levels in the control within non-fertilized plots were perhaps due to lower flower numbers in the same treatment. The effect of shelter under mulch and more flowers in these treatments, offering a richer source for pollen to adult parasitoids (Powell 1986; van Emden 1990), probably biased parasitoids' preferences towards mulch plots when no fertilizer was applied. Within fertilizer treatments the control, which counted more flowers in this case, yielded higher parasitization rates than both mulch treatments. *Dolichogenidea* sp. and *P. leucobasis*, which were found to attack early instars of *M. vitrata*, generally were more abundant in the control than in mulch during this season. The proportion of early instars to late instars was more elevated in the fertilized control, which possibly led to the comparatively high mortality rates. In turn, the proportion of late instars under mulch in fertilized plots was higher, explaining the relatively lower levels of parasitism. Again, proportions of larvae parasitized by *Dolichogenidea* sp. and *P. leucobasis* decreased over time in parallel with increasing proportions of *B. kriegeri*. The stage-dependence of several parasitoids, which evolve in changing proportions over time (Hawkins et al. 1990; Miller & Ehler 1990; Mills 1992; Ehler 1994) on successive larval instars, was thus demonstrated. One larva out of five was parasitized in pods by a tachinid fly, which generally attacked late instars.

Megalurothrips sjostedti

Although several alternative host plants with high potential for thrips development were found in the vicinity of cowpea (Fig. 7.8.), parasitism remained very low – at 0.2% on average. After suggestions of van Emden (1981) and Speight (1983), parasitism probably was reduced due to distribution in 12 different wild host plants around cowpea plots, the flowering cycle of which coincided with flowering of cowpea.

Third season (I/96)

Maruca vitrata

Parasitism in flowers, parasitoids in flowers, and parasitism in pods. Second instars recorded significantly the highest mortality rates and also revealed the highest proportion in terms of numbers compared with all other instars. It was shown that this second instar is most severely attacked (Table 4.37.) where parasitization incidences of *Dolichogenidea* sp. and *P. leucobasis* overlap. As Ehler (1985) reported, total parasitization levels increase with the number of different parasitoid species. This seems a plausible reason why this instar suffered the highest losses by parasitoids. In fact, this instar seemed to be the only stage where considerable attacks of more than one parasitoid exhibited their influence (Table 4.37.).

The second instar is proposed to be the stage of highest losses to the larval population. This is earlier than was proposed by Leumann (1994), who attributed highest losses to the third and fourth instar. This is conceivable if, as results by Arodokoun (1996) show, *Dolichogenidea* sp. is recorded with delay in the third and fourth instar. If sampled from early flowering as was done in the present study, *Dolichogenidea* sp. is left out less often, shifting the overlap with maximum losses towards earlier stages. However, this might depend greatly on different years and principally on the alternative host plant environment, which can have a strong influence on parasitoid abundance in cultivated crops (Way & Heong 1994). The first three instars recorded higher mortalities than the late instars. Early instars wander on the plant while moving from one to the next flower (Jerath 1968; Taylor 1978) and are highly susceptible to parasitoid attack. Later instars bore into pods where they are mechanically more protected and are attacked mainly by a single parasitoid, *B. kriegeri*. A tachinid fly was encountered rarely and levels reported by Arodokoun (1996) on the same parasitoid were very low, too.

Overall higher preferences by parasitoids for fertilized plots were observed supposedly responding to improved suitability of larvae for oviposition (Bentz et al. 1996). The observed NPK*mulch interaction basically separated the control and *Senna* from *Imperata* mulch. The difference between NPK levels for *Imperata* was emphasized most strongly. The ratio of early to late instars in non-fertilized plots in *Imperata* was relatively low at 1.8, and larval numbers were higher than for the control and for *Senna* without fertilizer. In turn, the ratio of early to late instars in fertilized treatments was also 1.8 in *Imperata,* but the abundance decreased slightly from non-fertilized to fertilized *Imperata*. For the control and *Senna*, NPK application resulted in an increased abundance, which was more emphasized for *Senna*. Within non-fertilized plots the control had the highest ratio of early to late instars (3.0) and about equal abundance as *Senna,* but was lower than *Imperata* in terms of larval numbers. The low mortalities in *Imperata* without NPK can be explained by a low ratio and relatively higher larval abundance. A lower proportion of early instars results in less parasitism since these early instars

were parasitized most. Higher overall larval numbers probably yielded reduced parasitism. Additionally, the pest population possibly grew faster than the antagonists' population (Lux, pers. comm.).

The high mortalities in the non-fertilized control probably were due to the high proportion of early instars, which are attacked most severely. *Senna* remained comparatively low in mortalities in fertilized plots although the ratio of early to late instars was 2.5. Relatively higher larval abundance compared with the control and *Imperata* could have reduced the efficiency of the parasitoids. The control had its maximum at DAP 49 and decreased thereafter, while both mulch treatments rose over three weeks (Table 4.23b.). Mulch probably was more favorable over time for parasitoids, giving shelter and thus increasingly encouraging parasitism. Whereas *Dolichogenidea* sp. remained at continuously low levels, *P. leucobasis* had its peak at DAP 49. At the same time *B. kriegeri* showed a setback but rose towards DAP 56. At DAP 42 the ratio of early to late instars was 7.1, which attracted *P. leucobasis* much more strongly. One week later, when larval numbers increased, the ratio was still 3.1 in favor of early instars.

This increase in larval numbers was due to emerging early instars, which even more strongly attracted *P. leucobasis.* At DAP 56 the ratio recorded 0.9, slowly shifting towards a dominance of late instars. The decline in proportion for *P. leucobasis* and increasing rates for *B. kriegeri* followed the expected change in age structure of the population followed by a shift in the parasitoids' community (Hawkins et al. 1990; Miller & Ehler 1990; Mills 1992; Ehler 1994; Sheehan 1994). Mortalities in pods did not suggest important variability and the dominant parasitoid was *B. kriegeri,* since an increasing proportion of late instars is to be expected in pods (Taylor 1978).

Megalurothrips sjostedti

Parasitoids were strongly attracted to fertilized plots, resulting in higher mortality levels of larvae of *M. sjostedti*. A nutritional effect was made responsible (Bentz et al. 1996). The interaction of mulch on both NPK levels indicated a stronger increase in *Senna* after fertilizer application, which could have been the result of less increase of larvae from non-fertilized to fertilized plots. The stronger increase of larval abundance in the control and *Imperata* through use of NPK probably could not be followed by the parasitoid, leading to reduced mortalities.

Fourth season (II/96)

Maruca vitrata

Parasitism in flowers, parasitoids in flowers, and parasitism in pods. The same situation applied for this season, which showed the same patterns of mortality for the different instars. The second instar revealed maximum mortalities and early instars were targeted more severely by parasitoids for the same reasons as discussed for season I/96. Again, fertilizer led

to a positive response by parasitoids, induced by increased suitability of larvae. For all instars together, the control recorded the most elevated mortalities, which can be explained with a higher ratio of early to late instars and lower larval abundance compared with both mulch treatments. Parasitization rates in *Senna* were lowest for early instars but highest for late instars, probably as the result of highest abundance of early larvae and lowest numbers of late stages in the same treatment. Parasitoid efficiency was expected to drop as pest numbers increased.

Mortality rates dropped from DAP 49 to DAP 56 as the ratio of early to late instars decreased from 2.6 to 1.2. Throughout the season, *P. leucobasis* was the dominant parasitoid responsible for high mortalities in early instars. As the proportion of later instars grew over time, *P. leucobasis* became less important and mortalities declined, leaving *B. kriegeri* as the single species to control larvae. This would suggest reduced mortalities as the number of species decreases (Ehler 1985). A comparison of non-fertilized with fertilized plots showed that the proportion of *Dolichogenidea* sp. and *P. leucobasis* increased while *B. kriegeri* declined. In NPK plots the ratio of early to late instars grew from 1.5 to 2.4, indicating an increased proportion of earlier larvae. Because better nourished plants are more suitable for larval development, oviposition of adults probably increased in these treatments. This caused the increase of early larvae, subsequently attracting *Dolichogenidea* sp. and *P. leucobasis,* which are principally attached to early instars (Table 4.37.).

Mortalities in pods were based on very few larvae only. The mortality patterns per instar followed those discussed in flowers. The few early instars that occurred in pods were attacked even more severely by *Dolichogenidea* sp. and *P. leucobasis,* which obviously do not restrict their search for hosts to flowers only.

Megalurothrips sjostedti

Parasitoids were more attracted to fertilized plots where larvae were assumed to be of better suitability for parasitoids' offspring (Bentz et al. 1996). Higher parasitism rates under mulch were ascribed to a shelter effect, which protects parasitoids from adverse climatic conditions (Baldy & Stigter 1993). However, the differences remained below 1.5% and were not considered biologically important.

Fifth season (I/97)

Maruca vitrata

Parasitism in flowers, parasitoids in flowers, and parasitism in pods. No parasitism was found for first instars. Mortality for second and third instars peaked at DAP 49 as the ratio of early to late instars (2.0) peaked, too. In parallel, the proportion of *P. leucobasis* reached its maximum (Fig. 4.32.), indicating that the population consisted of a high proportion of second

and third instars. These instars are highly susceptible to this parasitoid (Table 4.37.), together with *Dolichogenidea* sp., but the latter was of no importance during this season. The peak in mortality for early instars is to be explained mainly by the ratio of instars. The increase of mortality in late instars towards DAPs 63 and 70 was likely initiated at DAP 56 when the ratio of early to late instars fell to 0.5. This favored *B. kriegeri*, which attacks mainly late instars. *Dolichogenidea* sp. and *P. leucobasis* dropped in successes at the same time. After a week of high precipitation (DAPs 63-70) larval numbers increased again, possibly attracted by newly developing flower buds of a second flowering cycle, which turned into flowers after DAP 77 (Fig. 2.14.). This again increased the ratio of early to late larvae from 1.4 to 2.4 at DAP 63 and DAP 70, respectively. A slight increase of parasitism in second instars occurred (Table 4.30.) again due to *P. leucobasis* (Table 4.32.), which increased in proportions while *B. kriegeri* declined. This new flowering cycle attracted adults of *M. vitrata* for oviposition anew, leading to another new generation. *P. leucobasis* reacted positively to this rejuvenation of the population.

The interaction of mulch treatments between NPK levels indicated a difference in variation for *Imperata*, which was the inverse for the control and *Senna*. *Imperata* decreased in mortalities, whereas the control and *Senna* increased (Table 4.31a.). The increase was mainly ascribed to the fertilizer effect on larvae, which became more suitable for the parasitoids. The larval abundance for both treatments decreased slightly in NPK plots, too. This probably increased the number of successes by the antagonists. *Imperata* displayed an increase in larval abundance, which, in turn, possibly reduced successes of oviposition by the parasitoids. The ratio of early to late instars was lower in the fertilized plots and did not explain this phenomenon. Within non-fertilized plots, mulch showed higher mortalities due to a shelter effect for parasitoids, which could have biased their abundance (Baldy & Stigter 1993). Low larval numbers were found in pods and yielded only *B. kriegeri*. This parasitoid is more attached to late instars, which are principally found in pods (Taylor 1978).

Megalurothrips sjostedti

Fertilized plots attracted more parasitoids right from the beginning of flower sampling at DAP 42 (Table 4.33.). This was ascribed to a better suitability of the host, which created better conditions for oviposition (Fennah 1963; Lewis 1973; Ananthakrishnan & Gopichandran 1993; Bentz et al. 1996; Mollema & Cole 1996). The mortality peak followed one week after the peak in abundance of larvae when larval numbers began to decline. A strong increase of larval numbers between DAP 42 and DAP 49 (Fig. 3.10.) hardly resulted in increasing mortalities (Table 4.33.), as the larval population probably increased faster than the parasitoid population. In turn, the decline in larval numbers after the peak increased parasitization rates mainly due to an improving ratio of parasitoids to thrips larvae. Although larval abundance was higher in fertilized plots, mortalities were more elevated, too. Flowering started earlier in these treatments and possibly attracted the parasitoid earlier. The alternative host plant environment recorded an interrupted flower production (Fig. 7.11.) between DAP 28 and DAP 91, possibly

forcing the parasitoid to rely on cowpea flowers for pollen feeding of the adults (Powell 1986; van Emden 1990), the result of which may have led to these comparatively high parasitization rates. Alternative host plants, which contributed to the parasitoid population build-up outside the monitored area, are also probable sources for higher mortalities.

IITA

First season (I/95)

Maruca vitrata

Parasitism in flowers, parasitoids in flowers, and parasitism in pods. Few larval numbers and rare mortality events did not allow sound judgement during this season.

Megalurothrips sjostedti

Sampling revealed very few parasitized larvae at DAP 56 only, and the overall mortality rate remained below 0.5% for the season. Analysis was not possible.

Second season (II/95)

Maruca vitrata

Eggs. Parasitism rates at DAP 63 in the neem treatment were highest but remained lowest in *Imperata*. No relationship was found between parasitization rates and egg numbers since few eggs were exposed at roughly the same numbers among treatments. The mortality difference at DAP 63 tentatively was connected with larval abundance in the different treatments. *Imperata* recorded lowest mortalities, which occurred together with lowest abundance (Fig. 3.12.). *Imperata* also displayed the strongest decrease in abundance after DAP 56, indicating that the population collapsed and probably no further oviposition by *M. vitrata* took place. Therefore, *Trichogrammatoidea* sp. may have avoided this treatment and thus did not visit the carrier plants either. The neem treatment rose slightly in larval numbers between DAPs 56 and 63. Thus, oviposition still took place on plants. This might have stimulated the search of *Trichogrammatoidea* sp., which also oviposited in the eggs of the carrier plants. This attracting effect probably was stronger due to the mulch cover of the soil where the parasitoid found more favorable conditions (Baldy & Stigter 1993). This seems realistic compared with the control, which in parallel increased in abundance of larvae after DAP 56 but remained by far lower in mortality, not indicating an attractive effect of mulch. The control revealed comparatively high parasitization levels at DAP 70, but the levels dropped in the other treatments. At DAP 63

the control recorded about double the larval numbers than all other treatments, too. This indicated that oviposition by *M. vitrata* lasted comparatively longer and thus attracted *Trichogrammatoidea* sp. longer before they left this treatment.

Parasitism in flowers, parasitoids in flowers, and parasitism in pods. Low larval numbers in flowers with two larvae parasitized by *P. leucobasis* and *B. kriegeri*, respectively, did not allow any conclusions. No parasitism was observed in Pods.

Megalurothrips sjostedti

High thrips numbers prevailed in this season in cowpea (Fig. 3.12.) and alternative host plants in the neighborhood (Fig. 7.13.), but only two larvae were parasitized in total, resulting in a mortality rate of 0.06%. A relatively diverse habitat, which is required by adults of the antagonist (van Emden 1990; Altieri et al. 1993; van Driesche & Bellows 1996), and extremely high larval and adult numbers in flowers, would have suggested higher and more regular attacks by *Ceranisus menes.* Even if a higher diversity of host plants is likely to reduce parasitization levels through distribution (van Emden 1981; Speight 1983), these two mortality incidences at DAPs 49 and 63, respectively, rather indicate a de facto absence of the parasitoid.

Third season (I/96)

Maruca vitrata

Eggs. During this season, no relationship could be found between mortalities and egg numbers, larval abundance, or flower numbers. When considering the whole period when eggs were exposed on carrier plants, including the period before flowering (DAPs 28-42), higher mortalities were recorded in *Senna* and neem treatments. Since effects caused by different numbers of eggs on carrier plants could be excluded, higher mortalities in both mulch treatments were likely to stem from a shelter effect for parasitoids, as proposed by Baldy & Stigter (1993).

Parasitism in flowers, parasitoids in flowers, and parasitism in pods. Although a high abundance of larvae of *M. vitrata* prevailed in this season, only three incidences of mortality were recorded at DAP 56, resulting in overall 0.3%. The same applied for pods, where no parasitism was recorded despite relatively high larval numbers. Many cowpea plots, which were spread over the whole experimental area of IITA, served as resources where *M. vitrata* could build up its population. In turn, no alternative host plants were found in the vicinity of cowpea. The few parasitization incidences suggest that although the pest occurred abundantly, the environmental conditions were not favorable for the antagonists, which lacked alternative host plants whose presence is necessary as alternative sources for feeding and oviposition (Powell 1986; van Emden 1990; Way & Heong 1994).

Megalurothrips sjostedti

Six weeks of sampling revealed 29 parasitized larvae resulting in an overall mortality rate of 0.7%. As was mentioned for parasitism of *M. vitrata,* the abundance of host organisms in the context of a poor alternative host plant environment did not attract an important population of antagonists.

Fourth season (II/96)

Maruca vitrata

Eggs. This season yielded overall very few parasitized eggs, which were obtained at DAPs 56, 63, and 70. Egg numbers gained for DAP 63 were not sufficient and were not included in analysis. At DAP 56 *Imperata* and neem mulch recorded mortalities, whereas the control and *Senna* showed no parasitism. *Senna* and neem mulch yielded parasitized larvae at DAP 70, when the control and *Imperata* did not. This season was particularly dry and did not receive rainfall after DAP 42. Mortalities, which were found in mulch treatments only, suggest a beneficial effect of mulch for the parasitoid (Baldy & Stigter 1993). Rising temperatures after the last rainfall (Fig. 3.14a.) together with increasing drought probably biased the parasitoid population towards more humid and cooler microenvironments under mulch, where the only mortalities were recorded.

Parasitism in flowers, parasitoids in flowers, and parasitism in pods. Very low larval abundance was recorded in flowers with one incidence of mortality, which has to be ascribed to chance. No parasitism was observed in pods where only two larvae were collected. Although *Centrosema pubescens* accompanied cowpea cultivation throughout the season (Fig. 7.15.), the parasitoid populations were not attracted by the particular environment.

Megalurothrips sjostedti

As observed for *M. vitrata* larvae, the only parasitization incidence did not suggest a stable population of the parasitoid. The overall parasitization rate remained at 0.03%.

Fifth season (I/97)

Maruca vitrata

Eggs. *Senna* recorded a steady increase in larval abundance between DAP 42 and DAP 56 (Fig. 3.15.), when permanent oviposition by *M. vitrata* occurred. This availability of eggs probably attracted *Trichogrammatoidea* sp., resulting in higher mortalities of eggs on the carrier plants. The steep increase of larval numbers in the neem treatment was caused by a high oviposition rate. In parallel, the mortalities on eggs of the carrier plants declined. The high in-

crease of resources is assumed to reduce the relative number of successes for oviposition of the parasitoid, which probably explains the decline in mortality. No relationship was found between mortalities and exposed egg numbers as well as flower numbers. As for the second part of the data covering DAPs 63-77, very few eggs were parasitized. Their distribution among the different treatments did not permit analysis. However, across the three weeks a tendency of parasitism towards mulch treatments was observed. This suggested a beneficial effect of mulch (Baldy & Stigter 1993), which possibly biased parasitoid activity towards mulch treatments.

Parasitism in flowers, parasitoids in flowers, and parasitism in pods. Very few parasitized larvae were obtained from flowers. Although no significant differences were found between treatments, mulch treatments tendentiously revealed more than double the parasitization rates of the control. This was ascribed to more favorable conditions for parasitoids to find shelter under mulch, as proposed by Baldy & Stigter (1993). However, these differences were small on overall very low mortality rates and therefore not regarded as biologically important. The population of *M. vitrata* larvae consisted of an almost 2-times higher proportion of earlier to later larvae at DAP 49, explaining that except for a single *B. kriegeri* the early attacking parasitoids *Dolichogenidea* sp. and *P. leucobasis* were isolated. As the population grew older (DAPs 56, 63), the structure shifted to an increasing proportion of later instars, which were attacked by *B. kriegeri* only. This shows the specific response of a parasitoid guild to fluctuation and changes in the age of the host (Jaksié 1981; Askew & Shaw 1986; Hawkins & MacMahon 1989; Miller & Ehler 1990; Hirose 1994; Mills 1994; Sheehan 1994). Parasitization rates increased from DAP 49 to DAP 63 as the population decreased. This might increase the successes of the parasitoid, which, in turn, reaches its highest incidences towards the end of the cultivated crop (Otieno et al. 1983). Parasitism in pods was very low, and except for a single *P. leucobasis*, *B. kriegeri* hatched out of larvae. This was to be expected as the proportion of late instars in pods predominate (Taylor 1978).

Megalurothrips sjostedti

The overall parasitism rate remained at 0.2%. The distribution of attacked larvae over treatments did not allow a sound analysis. Mortality rates increased slightly from DAP 49 to DAP 56 but decreased again as the thrips population grew faster between DAPs 56 and 63. This was probably too fast for the generally delayed growth of parasitoid populations (Greathead 1987).

Conclusions

Five influences were reckoned to be of crucial importance for parasitism on eggs of *M. vitrata* on exposed carrier plants and larvae of *M. vitrata* and *M. sjostedti* in flowers and pods of cowpea. These were host plant environment, qualitative properties of the plant, larval age,

larval abundance, and physical aspects of refuge for antagonists. All of them interacted to a varying degree and made it almost impossible to obtain clear results on their main effects.

Host plants generally divided the three regions in terms of diversity and potential species being preferred by both pests. Although pests responded highly positively to almost year-round cowpea cultivation on the experimental sites at IITA, their antagonists were not able to develop a population due to lack of undisturbed diverse habitat. Despite comparatively more alternative host plant species in Tokpa/Ayou, the prevailing land pressure in southern Benin resulted in a low proportion of trees but comparatively more shrubs, which often did not reach the flower stage. Although regular bush fires during the long dry season in Lema eliminated the ground cover almost entirely, most of the trees were hardly affected and recovered quickly. This south-north gradient in vegetational characteristics appeared to be responsible for higher parasitization rates in Lema and the de facto non-existence of antagonists in some seasons at IITA.

The improved nutritional quality of the plants after NPK application exerted a positive influence on parasitization rates, which was ascribed to a positive response of parasitoids to the modified metabolism of larvae feeding on fertilized plants. When assessed over time, the acceleration of growth and senescence of fertilized plants became visible in parasitization rates due to nutritional preferences of pests' larvae.

Depending on the age structure of the larval population of *M. vitrata*, considerable differences in mortalities were observed. The younger the population, i.e., the higher the proportion of early instars, the higher the losses ascribed to attacks by parasitoids. Given the specific preferences of mainly three species of the parasitoid guild, the overlap of two species – *Dolichogenidea* sp. and *P. leucobasis* – remarkably increased losses of early instars (first to third) through mortality. With increasing age of the population, only one species remained, *B. kriegeri*, resulting in a nominal decrease of mortality. In addition, the biology of the larvae could explain that early instars are more susceptible to attacks while wandering on the plant, whereas later instars bore into pods and are thus mechanically protected to a high degree from parasitoids. Taking into consideration the oviposition preference of different parasitoids for specific host instars, an estimation of the population structure is possible on the basis of ovipositional proportions among the parasitoid species.

Although behavioral aspects of the parasitoids under study are not known, a negative density dependent parasitization rate of these species was proposed. Increasing numbers of pests resulted in increasing numbers of parasitized larvae up to a certain limit, after which the numbers increased slowly or dropped. Parasitism rates thus increased or remained stable until larval numbers reached a limit from where these rates declined. Seasonal effects resulting in an accumulation of pests during the year, backed these assumptions in particular. This phenomenon of density dependence was more pronounced for *M. vitrata*, where mortality rates reached by far higher levels than for *M. sjostedti*. Several cases occurred in which low larval abundance did not result in high mortalities. Based on the reflections of van Emden (1981) and Speight

(1983) that many plant species can lead to a reduction in parasitization rates through distribution, it might be conceivable that too few larvae per given number of resources (e.g., flowers) may yield similar effects while reducing the chance for encounter between parasitoid and prey.

Results of Arodokoun (1996), who stated that *P. leucobasis* is more strongly attracted to high growing hosts like trees and *B. kriegeri* is dominant on low hosts, e.g., cowpea, could not be confirmed. The study revealed the opposite, indicating that *P. leucobasis* in general was the dominant parasitoid in cowpea compared with *B. kriegeri* and *Dolichogenidea* sp. Regional comparisons between the three parasitoids revealed a ratio of 0.07:0.25:0.68 (*Dolichogenidea* sp.: *P. leucobasis*: *B. kriegeri* [proportions summing to one]) for IITA, 0.03:0.51:0.46 for Tokpa/Ayou, and 0.12:0.69:0.19 for Lema. Although *B. kriegeri* indeed was the dominant parasitoid at IITA, this was not the case for Tokpa/Ayou and Lema. While IITA is characterized by a highly disturbed habitat, Lema is distinguished by higher proportions of trees and recorded the highest proportion of *P. leucobasis*. Findings by Arodokoun (1996) suggest that high hosts like *Pterocarpus santalinoides, Lonchocarpus sericeus,* and *L. cyanescens* indeed might be more suitable for *P. leucobasis* compared with cowpea. However, these results seem to be biased by the vicinity of the high host. In close presence of these high hosts, *P. leucobasis* is probably underrepresented in cowpea while being more attracted to the alternative host. In the case of the present study, none of these trees was found in the nearby environment.

The effect of mulch offering shelter to parasitoids and thereby biasing the population towards *Senna* or *Imperata* treatments was considered very weak and only appeared when all other influences could be excluded. The controversy over the impact of mulch on insects probably persists because other influences, some of them discussed above, are stronger and more specific. Influences like nutrition (NPK, host plants) or host specialization (instars), which have direct implications for reproduction of the antagonist population, are possibly of higher importance than shelter for the adult.

The rare cases in which mulch resulted in higher larval mortalities as well as the mostly low rate of increase under mulch suggest that mulching in the quantities used in the present study was not an appropriate tool for controlling pests. This was especially true for thrips, which were regarded as the dominant pest during the whole experimental period. Extremely low mortalities were hardly improved since even two- or threefold increases in parasitization rates resulted in rates below 4%. Despite their statistical significance, these rates remained biologically insignificant. Factors that dominantly influenced parasitism rates were alternative host plants and the age structure of the larval population, which also determined the total pest densities in cowpea. Human impact on the host plant environment, as in the case of IITA with its urban setting, probably resulted in the most severe impact on the pest-antagonist complex.

5 Pod damage to cowpea ascribed to attacks by *Maruca vitrata* under different mulch treatments in combination with chemical fertilizer NPK

ABSTRACT Throughout its development cycle, cowpea, *Vigna unguiculata* (L.) Walp. (Leguminosae), is the target of pre-flowering, flower, and post-flowering damages caused by a complex of several pests. The focus of this study was to assess the damage to pods that is attributable to *Maruca vitrata* F. (Lepidoptera: Pyralidae) alone. Plants were harvested repeatedly over time in three different regions of Benin – Tokpa/Ayou, Lema, and IITA Station – to investigate variation between treatments consisting of different mulch types and chemical NPK fertilizer. Total pod numbers, pod weight, number of attacked pods, and quantity of grains were measured to account for damage, and an estimator was created to judge the total yield loss on pods. A repeated measures approach allowed comparisons of trends in damage over time. Pod damage was influenced principally by larval abundance in flowers and pods in combination with number of pods per unit, which permitted calculations of larval densities. As late instars were regularly found in flowers, it was suggested that migration to pods is not necessary for the completion of larval development. Grain damage also depended on larval abundance determining the number of larvae feeding on the same pod. The ratio of late to early instars assisted in explaining increased grain damage through prolonged presence of larvae in pods. Precipitation influenced pod ripening, which decides on the suitability of the food source for larvae. Continued rainfall delayed the ripening process and thus led to increased grain damage over time. Pod weight, which is correlated with seed number and size as well as pod length, helped in interpreting grain damage in relation to pod size. Total yield losses caused by *M. vitrata* on pods alone did not reach important levels and were of low economic significance.

Maruca vitrata is only one among several pest species that damage cowpea pods and hence lead to yield loss. Although its damage can be easily traced due to typical frass residues (Taylor 1967), this tells little about the real damage potential of the pest, which competes for the same resources with other post-flowering pests (Dreyer & Baumgärtner 1995). The most important yield losses in cowpea are probably caused through flower damage by the flower thrips *Megalurothrips sjostedti* Trybom (Thysanoptera: Thripidae), which occurs before pods are set. This masking effect (Jackai & Singh 1991) makes it difficult to judge on the real damage potential of a complex of subsequent post-flowering pests. Every approach that aims to assess damage by a single pest species contains shortcomings (Dreyer & Baumgärtner 1995), which necessarily bias the results as the interactions with the other pests in the complex are not accounted for. However, the present study focused on comparative investigation of damage and did not attempt to assess the damage potential of *M. vitrata*.

Odulaja & Oghiakhe (1993) considered flower infestation and larval abundance as suitable descriptors for yield loss in cowpea. Karel (1993) reported that increasing plant densities of common beans reduced damage to pods. This can be attributed to reduced larval densities on the basis of an increase of plants and therefore pods per unit.

Various studies focused on anatomical and biochemical parameters of resistance to *M. vitrata* on cowpea or between different cultivars (Tayo 1989; Oghiakhe et al. 1992a,b, 1993b) to explain damage on the basis of plant-borne parameters. However, factors like larval abundance, larval age, pod size, and, to a limited extent, climatic conditions are suggested to be of importance when discussing pod damage in general.

The extent to which mulch or NPK application can directly influence damage patterns in pods or grains, or affect plant growth or pest abundance, is discussed in this study.

Materials and Methods

Beginning with the time of early pod formation, weekly samples on 10 plants per treatment were collected (the same day as all other exercises). Random numbers were used to select the plants, which were harvested entirely and marked thereafter with a colored ribbon. Subsequent pod sampling on the marked plants was avoided. All pods of the 10 plants were assigned to one envelope (33.5 x 16.5 cm/ 13 g; 45 x 20.5 cm/ 25 g – length x width/ weight for two sizes). During the counting in the laboratory, pods were systematically searched for the boreholes that are typical of damage by the pod borer (Taylor 1967). All attacked pods were counted and opened, and grains were counted per pod. All pods per treatment (not attacked plus attacked) were put back into envelopes, dried in the oven (80°C for 96 hours or 105°C for 72 hours) and weighed thereafter. The measures thus gained were: total number of pods per 10 plants, number of attacked pods per 10 plants, number of grains per attacked pods, number of damaged grains per attacked pods, weight of pods (dry matter) per 10 plants, weight per pod. As a further step, the estimated yield loss attributed to *M. vitrata* was calculated on the basis of total number of pods, number of attacked pods, and number of damaged grains per attacked pod:

$$\text{Estimated yield loss} = \frac{\text{number of attacked pods x number of attacked grains}}{\text{total number of pods x total number of grains}} \text{x} 100$$

Because of the often-high number of pods, it was not possible to count grain numbers in all the pods that were harvested regularly in all treatments. As a subsample, the grain numbers of attacked pods were used as multiplier for non-attacked pods. The set-up of final grain numbers is among the first steps during pod formation in leguminous plants and influence of damage by the pod borer on their number can thus be excluded.

The sampling dates for pod harvest were equally spaced and allowed application of repeated measures analysis (ANOVAR) (Greenhouse & Geisser 1959; Huynh & Feldt 1970; Hand & Taylor 1987; Potvin et al. 1990; Vanleeuwen et al. 1996). Mean scores of pods per 10 plants were used as responses. For analysis on total numbers of pods, weights per pod, and estimated yield losses, ANOVAR for mixed models was carried out, using polynomial trend contrasts for profile analyses. *F*-values were marked with $^{[l]}$,$^{[q]}$, or $^{[c]}$ if tested on the linear (first order polynomial), quadratic (second order polynomial), or cubic trend (third order polynomial), respectively. Data for total pod numbers and weights per pod were $\sqrt{(x + {}^{3}/_{8})}$ transformed and those for estimated yield losses to arcsine $\sqrt{p}$ if necessary (after investigation of standardized residuals). *A priori* chosen contrasts and least squares means (LSMeans) served as tools for mean separation after ANOVAR.

The ratio of attacked pods and grains per attacked pods was analyzed using GENMOD in SAS to adjust for different sample sizes due to varying numbers of pods per plant. The raw data for numbers of total and attacked pods have thus been used instead of the proportion. The results for attacked pods were thereby weighed for the respective sample size (number of total pods). On the basis of the generalized linear models (GLIM) (Nelder & Wedderburn 1972; Liang & Zeger 1986; Dobson 1990; Diggle et al. 1994; Lipsitz et al. 1994), repeated measures were applied, accounting for the particular covariance structure of the data, which was assumed as to be autoregressive (Box 1954; Kenward 1987; Legendre 1993). While using GENMOD, data were logit transformed, recognizing their binomial distribution. After the likelihood-ratio statistics (Chi-square), which was used to test for treatment effects, *a priori* chosen contrasts assisted in separating means. Since GENMOD (SAS) does not furnish appropriate output that could be used for presentation, the statistical package GENSTAT was used on the same model to obtain detransformed mean ratios with standard errors of the means (Korie, pers. comm.). Responses on damage to pods and grains were expressed in detransformed percentage ± standard error of the mean (SEM).

After each ANOVAR, least squares means were conducted for separation of means. To account for *a priori* chosen treatment differences, orthogonal contrasts were selected. Since contrasts can represent combinations of comparisons as “weighted sum of means” (Hand & Taylor 1987, p. 10), they were used to compare different clusters, e.g., first growing seasons (I/95, I/96, I/97) against second growing seasons (II/95, II/96) or no mulch (control) versus mulch ([*Senna siamea* (called *Senna*) + *Imperata cylindrica* (called *Imperata*)]/2).

To distinguish seasonal and regional patterns, factorial analysis across time was preferred over repeated measures. Particularly distinct profiles within each season and between first and second rainy seasons did not allow proper comparisons of trends. Instead, seasons and regions were incorporated as additional factors. For comparisons between regions and between seasons within regions, replications were nested within region and season, respectively, to use a hierarchical error term (Korie, pers. comm.).

A *P*-value of 0.05 was generally used to judge on significance although higher levels were considered as marginal responses if reckoned important. c^2- and *F*-values were marked with one star (*) if $0.05 > P \geq 0.01$ and with two stars (**) if $P < 0.01$.

The exact description of experimental sites and the research design, auxiliary data like climate and soil properties, and a detailed description of the statistical approach were discussed completely in Chapter 1 and may assist in further understanding.

Results

Regional differences

NPK was not used at IITA. Hence, regional differences were tested in two steps. An overall comparison of the three regions did not consider NPK, leaving mulch as the single treatment factor. The neem treatment at IITA was excluded as well, as it was a special component of the on-station trials only. A second step compared the two on-farm regions Tokpa/Ayou and Lema, controlling for NPK.

All regions

Total pod numbers. Total numbers of pods, which were harvested weekly on 10 plants per treatment, did not reveal distinct regional or seasonal patterns. Regions differed during the first growing seasons only (Table 5.1.). During these three seasons, Lema always resulted in significantly inferior pod numbers compared with IITA and Tokpa/Ayou, the two of which did not vary significantly one from the other ($F = 8.4^{**}$).

Total pod yield. Measurement of pod weight was started in season I/96. During season I/96, Tokpa/Ayou yielded significantly more pods than IITA and Lema, the latter two did not reveal significant differences ($F = 10.6^{**}$) (Table 5.2.). During season II/96, Lema recorded highest pod weights and was significantly superior to Tokpa/Ayou. Lema yielded significantly lowest in season I/97 compared with IITA and Tokpa/Ayou, which did not differ significantly from each other.

Pod weight. The patterns for weight per pod were identical to the results found for total pod yield (Table 5.3.). In season I/96, Tokpa/Ayou recorded significantly heaviest pods (0.4^d g per pod) compared with IITA (0.2^d) and Lema (0.2^d), which were similar in weight ($F = 13.9^{**}$). Season II/96 favored Lema (0.4^d) compared with Tokpa/Ayou (0.2^d), IITA (0.3^d) was in between. Season I/97 led to heavier pods in Tokpa/Ayou (0.4^d) and at IITA (0.5^d), which was significantly superior to Lema (0.1^d).

Relative pod damage. Damage caused by *M. vitrata* larvae was not distinct among regions. Mulch rather differed between regions IITA and Lema ($c^2 = 29.8^*$) (Table 5.4.). *Senna*

exhibited lowest damages at IITA contrasting the control and *Imperata*, which were close together. In Lema, the control scored lowest compared with both mulch treatments, *Senna* and *Imperata*, which recorded about the same damage. Whereas the control in Lema showed lower damage than mulch treatments, the opposite was the case in Tokpa/Ayou where the control revealed the highest attacks. Season II/95 was not included in the analysis since only rare events of damage in all regions were recorded.

Relative grain damage. A distinct variation between regions indicated that Tokpa/Ayou scored significantly lowest (24.3^{d}% attacked grains per pod) in contrast with IITA (27.2^{d}) and Lema (30.1^{d}), both of which were not significantly different ($c^2 = 18.5^{**}$).

Estimated yield loss. Regional differences were not significantly distinct. Variation between regions was different on a seasonal basis ($F = 17.1^{**}$) (Table 5.5.). In season I/95, total yield losses at IITA (3.0^{d}%) were significantly more than in Tokpa/Ayou (1.3^{d}) and Lema (0.1^{d}), the latter two did not show significant variation between them. Seasons II/95 and I/96 recorded similar results between regions but during season II/95, few events of attacks lead to almost no losses. Lema (3.6^{d}) displayed highest yield reduction in season II/96 and was significantly different from Tokpa/Ayou (0.1^{d}) and IITA (0.0^{d}). In season I/97, all three regions were significantly different from each other. Tokpa/Ayou (6.4^{d}) showed highest losses compared with IITA (3.0^{d}) and Lema (0.5^{d}); Lema scored lowest.

On-farm regions

Total pod numbers. Whereas no significant increase in pod numbers in Lema could be achieved through NPK fertilizer (24.2^{d} pods per 10 plants without, 27.3^{d} with NPK), this did occur in Tokpa/Ayou (55.9^{d} without, 75.8^{d} with NPK) ($F = 5.0^{*}$). An assessment of seasonal differences showed no significant variation for seasons I/95 and II/95, but in seasons I/96, II/96, and I/97, fertilizer significantly increased pod numbers ($F = 7.3^{**}$).

Total pod yield. The pod yield per 10 plants increased by almost 70% across both regions with fertilizer application ($F = 5.1^{*}$).

Pod weight. NPK did not have an impact on the weight of pods across regions and seasons.

Relative pod damage. NPK led to different results in seasons between regions. Seasons I/95 and I/97 showed less damage in Lema in fertilized plots, whereas in turn fertilizer application resulted in higher borer damage during seasons I/96 and II/96 ($c^2 = 17.9^{**}$). Fertilizer increased damage levels in Tokpa/Ayou except for season I/96, where NPK led to reduced attacks. Season II/95 was discarded from analysis due to rare events of damage.

Relative grain damage. NPK did not reveal a general impact on grain damage across regions and seasons.

Estimated yield loss. The losses due to *M. vitrata* larvae were significantly higher in both regions across seasons when fertilizer was applied (1.3^{d}%), in contrast with plots without NPK (0.9^{d}) ($F = 4.1^{*}$).

Seasonal differences within the same region

Tokpa/Ayou

Total pod numbers. Highest pod numbers were always yielded in the first growing seasons (Table 5.6.). This was significantly more than during second growing seasons ($F = 50.3^{**}$). Within the cluster of early seasons, I/95 did not significantly differ from seasons I/96 and I/97, but I/96 counted more pods than I/97. No difference occurred between late cropping seasons. Within non-fertilized plots, season I/95 was close to I/96 and the late seasons did not differ significantly from each other ($F = 54.1^{**}$, simple effects). When fertilizer was applied, early seasons deviated significantly from late seasons, but no differences were found within each cluster ($F = 27.1^{**}$). Generally, fertilized treatments resulted in significantly higher pod numbers ($F = 14.0^{**}$).

Total pod yield. Weighing pod yields was started with season I/96. Yields were significantly higher during early seasons, which did not differ greatly among each other ($F = 27.5^{**}$). NPK had no significant impact on yield.

Pod weight. Similar to yield patterns, pods were significantly heavier during early seasons compared with season II/96 ($F = 11.4^{**}$). Within early seasons, no significant variation occurred. NPK did not influence pod weights.

Relative pod damage. Variation occurred among seasons, with I/97 recording significantly highest attacks compared with seasons I/95, I/96, II/96, and II/95 ($c^2 = 1{,}353.1^{**}$) (Table 5.7a.). Seasons II/95 and II/96 did not deviate from each other but scored significantly less than seasons I/95 and I/96 – the latter was significantly inferior to season I/95. Seasonal damage interfered with NPK levels in the way that NPK significantly increased damage in seasons I/95, II/96, and I/97, while attacks were reduced during seasons II/95 and I/96 ($c^2 = 17.5^{**}$). Within non-fertilized treatments, season II/95 did not significantly vary from season II/96 ($c^2 = 439.2^{**}$, simple effect), but within fertilized plots, all seasons significantly differed from each other ($c^2 = 1{,}053.9^{**}$, simple effect). Mulch also resulted in variation, which changed among seasons ($c^2 = 18.8^{*}$). A comparison of the control with *Imperata* mulch showed that damage levels did not significantly differ between season I/95 versus II/95 and II/96, but the other seasons showed different patterns (Table 5.7b.). This effect was due principally to lower scores for the control in seasons I/95 and II/96, whereas the other seasons had higher damage levels in the control than *Imperata*. *Senna*, which contrasted with *Imperata* mulch, recorded differences in patterns between season I/95 versus I/96 and I/97, as well as season II/96 versus I/96

and I/97. Lower values in seasons I/95 and II/96 in *Senna* compared with *Imperata* were mainly responsible for this interaction. In general, the control recorded highest damages in seasons II/95, I/96, and I/97, while *Imperata* scored highest during seasons I/95 and II/96.

Relative grain damage. Uniquely seasonal variation occurred when assessing losses to grains ($c^2 = 35.2^{**}$). Season II/95 (39.1^{d}% grain loss per pod) and I/97 (30.9^{d}) were not significantly distinct from each other, but both showed significantly more damage than seasons II/96 (22.8^{d}), I/95 (22.6^{d}), and I/96 (20.8^{d}). The latter group did not show differences.

Estimated yield loss. Seasons resulted in different estimates for yield loss. Early seasons recorded significantly higher losses than late seasons ($F = 23.9^{**}$). Within the cluster of early seasons, the most elevated damage was found in season I/97 (6.4^{d}% yield loss), which was significantly higher than for seasons I/96 (3.1^{d}) and I/95 (1.3^{d}). Losses in season I/96 were also significantly higher than in season I/95. Within late seasons, no significant variation occurred between seasons II/95 (0.03^{d}) and II/96 (0.1^{d}).

Lema

Total pod numbers. Significantly more pods were produced in I/96 than in seasons I/95, II/95, and I/97 ($F = 4.2^{*}$). The latter three seasons did not reveal significant variation among each other. Season II/96 yielded numbers in between I/96 and the remaining seasons and did not show differences from all other seasons.

Total pod yield. Measuring pod yield was started with season I/96. Marginal variation between seasons due to NPK levels occurred, indicating that during seasons I/96 and II/96 fertilizer increased pod yield, whereas during season I/97 yields dropped when NPK was used ($P \geq 0.05$).

Pod weight. Season II/96 (0.4^{d} g per pod) resulted in significantly heaviest pods compared with seasons I/96 (0.2^{d}) and I/97 (0.1^{d}) ($F = 3.7^{**}$). The two early seasons did not show significant variation between them.

Relative pod damage. Season II/95 was discarded from analysis due to the rare events of damage, which did not permit proper analysis. Seasonal comparisons marked season II/96 with significantly highest attacks compared with all other seasons ($c^2 = 183.7^{**}$) (Table 5.8.). Season I/96 also recorded significantly more damage than seasons I/95 and I/97, and the latter two did not greatly differ from each other.

Relative grain damage. Mulch treatments were attacked inversely among seasons ($c^2 = 47.2^{**}$) (Table 5.9.). Investigating the control versus mulch types, *Senna* and *Imperata* in season I/95 showed significantly different patterns than in seasons I/96, II/96, and I/97. Season I/96 also recorded differences compared with I/97. This differing order is due principally to the fact that the control resulted in lower damage levels than mulch in seasons I/95 and I/97, whereas the opposite appeared for seasons I/96 and II/96, which revealed higher damage in the control. This inverse composition was most accentuated among seasons I/95 and I/96.

Estimated yield loss. Damages by *M. vitrata* led to significant variation among seasons ($F = 29.2^{**}$). Seasons I/96 (2.4^{d}% estimated yield loss) and II/96 (3.6^{d}) recorded similar levels but were significantly superior in losses to seasons I/95 (0.2^{d}), II/95 (0.0^{d}), and I/97 (0.6^{d}). Season I/95 did not differ significantly from seasons II/95 and I/97, but I/97 revealed significantly more damage than season II/95. Events for II/95 were very rare and still were zero when rounding to two digits after the decimal point. Across seasons, an impact of NPK fertilizer on losses was uncovered, indicating about 100% more losses due to fertilizer application (1.2^{d}) ($F = 4.2^{*}$).

IITA

Total pod numbers. Pod numbers per 10 plants were not remarkably different among early growing seasons but the whole cluster reached significantly higher numbers than both late seasons ($F = 50.6^{**}$). Within late seasons, significantly more pods were counted during season II/95 than II/96.

Total pod yield. Recording pod yields was started with season I/96. Both early seasons resulted in significantly higher pod yield than the late season II/96 ($F = 7.0^{*}$).

Pod weight. No significant variation was found between seasons or treatments. However, pods appeared to be slightly heavier in season I/97 (0.5^{d} g per pod) followed by II/96 (0.3^{d}) and I/96 (0.2^{d}).

Relative pod damage. Seasons II/95 and II/96 were not included in the analysis because they yielded only rare incidences of pod damage. Among mulch treatments, *Senna* mulch recorded significantly fewer damaged pods than the control and *Imperata* ($c^2 = 12.5^{**}$) (Table 5.10.). The other treatments did not vary significantly.

Relative grain damage. No significant variation appeared due to seasons or treatments. The overall damage level was 28.8^{d}%. Season I/95 resulted in slightly higher losses (30.9^{d}) compared with I/96 and I/97, both at 27.0^{d}%. Among mulch treatments, *Senna* recorded damages of 31.8^{d}%, followed by neem (29.8^{d}), *Imperata* (29.5^{d}), and the control (24.7^{d}).

Estimated yield loss. First growing seasons yielded significantly more losses than both second seasons ($F = 35.2^{**}$). Seasons I/95 (3.0^{d}%), I/96 (2.3^{d}), and I/97 (3.3^{d}) did not significantly differ among each other, as was the case for seasons II/95 (0.03^{d}) and II/96 (0.004^{d}).

Differences within seasons

Tokpa/Ayou

First season (I/95)

Total pod numbers. Mulch yielded different pod numbers when combined with NPK. The control and *Senna* produced inverse pod numbers on NPK levels compared with *Imperata* ($F = 4.2^{*}$) (Table 5.11.). The control resulted in lowest pod numbers within non-fertilized plots, whereas *Imperata* scored lowest when fertilizer was applied. *Senna* without NPK counted fewer pods than *Imperata,* but the opposite happened in the fertilized plots. Within non-fertilized plots, the control scored lowest and was marginally lower than *Imperata* ($P \geq 0.05$). Counts for fertilized plots separately gave *Imperata* the lowest pod numbers and were marginally lower than *Senna* ($P \geq 0.05$). The increase in the control due to fertilizer was significant. In general, the control and *Senna* gained in pod numbers when combined with NPK but *Imperata* decreased at the same time.

Relative pod damage. NPK levels in mulch treatments as well as over time differed on trends. *Senna* and *Imperata* yielded inverse damage patterns due to fertilizer application ($F = 10.4^{**}$) (Table 5.12.). While attacks in *Senna* could be reduced through NPK, pod damage was almost doubled in *Imperata* when fertilizer was used. In general, damage in fertilized plots was less for the control and *Senna*, whereas the effect for *Imperata* was the opposite. A linear trend difference for NPK profiles was obtained ($F = 9.5^{[l]**}$) (Table 5.12b.). Profiles with NPK started with twofold higher damage levels at DAP 56, peaked higher at DAP 63, but fell below the levels of non-fertilized plots at DAP 70.

Relative grain damage. Treatments had no impact on grain damage. While 15.6^{d}% grain losses were counted at DAP 56, losses increased to the maximum at DAP 63 (26.9^{d}) and fell slightly to 22.7^{d} one week later.

Estimated yield loss. Yield losses did not significantly vary between treatments. The yield losses reached 0.3^{d}% at DAP 56, increased to 2.5^{d} at DAP 63, and dropped to 1.6^{d} one week later.

Second season (II/95)

Total pod numbers. *Senna* and *Imperata* displayed inverse patterns due to NPK levels ($F = 3.3^{*}$): damage levels in *Senna* dropped with fertilizer application while they increased for *Imperata*. In general, levels increased in the control and for *Imperata,* but fell in *Senna* in fertilized plots.

Relative pod damage. Few events of pod damage were recorded. One happened at DAP 63 and the remaining occurred at DAP 70, which was analyzed separately. Damage pat-

terns for mulch varied with NPK levels ($c^2 = 604.3^{**}$). No damaged pods were found in *Senna* without fertilizer and, in turn, *Senna* alone was target of pod borer attacks in fertilized plots.

Relative grain damage. The few occurring events made it difficult to obtain a reliable analysis. Tentative results suggested more accentuated damage in fertilized plots (53.3^{d}%), contrasting with blank plots (28.4^{d}) ($c^2 = 4.4^{*}$). However, these results have to be regarded with caution.

Estimated yield loss. The yield loss followed the patterns that were found for pod damage and could be analyzed for DAP 70 only. Results indicated no losses in *Senna* without fertilizer and 1.1^{d}% for the control and 0.6^{d} for *Imperata*, all without fertilizer. In turn, no attacks occurred on pods in the control or in *Imperata,* and within fertilized plots, neither showed losses. *Senna* lost 1.0^{d}% of its yield ($F = 4.6^{*}$).

Third season (I/96)

Total pod numbers. Pod numbers differed among mulch types according to NPK levels over time (DAP) ($F = 2.6^{*}$). Since this three-way interaction was complex, it was split into simple effects. Within non-fertilized plots, *Imperata* produced significantly fewer pods than the control and *Senna;* they did not vary significantly from each other ($F = 6.5^{**}$, simple effect). No significant variation occurred among mulch on both NPK levels separately.

Total pod yield. Across DAPs 56-70, pod weight was significantly higher in fertilized plots than in non-fertilized ones ($F = 11.3^{**}$). Among mulch treatments, the control yielded significantly higher total pod weights than *Imperata* ($F = 4.9^{*}$). Yields for *Senna* remained in between.

Pod weight. Significant impact of treatments on pod weights was not observed. Pods weighed 0.1 g per pod at DAP 56 and increased to 0.6 and 1.2 g, respectively, during the following two sampling weeks.

Relative pod damage. A three-way interaction between NPK, mulch, and time (DAP) was significant ($c^2 = 23.7^{**}$) (Table 5.13.). For better understanding, simple effects within both non-fertilized and fertilized plots were investigated. Generally, the control showed different patterns on trends versus profiles of mulch. Within non-fertilized plots, the control differed from *Senna* in the first order polynomial and from *Imperata* in the second order ($c^2 = 17.9^{**}$). Within fertilized plots, the control varied on the quadratic trend versus mulch treatments ($c^2 = 13.5^{**}$). In terms of the simple effects without fertilizer, the control started with lowest damages at DAP 56, followed by *Senna* and *Imperata*. The control peaked in coincidence with *Senna* at DAP 63, while *Imperata* had its low. *Senna* fell below the levels of the other two treatments at DAP 70.

In the fertilized plots, the control started highest, peaked highest one week later, and fell below levels for mulch. *Senna* increased constantly to its maximum at DAP 70. *Imperata* recorded lowest losses at DAP 56, peaked in between the control and the level for *Senna* and joined the niveau of *Senna*. The basic interactions due to NPK fertilizer were the inverse onset

of the profiles for the control and *Imperata,* as well as the inverse levels for profiles during the three weeks between the control and *Senna*. Application of NPK fertilizer increased damages in the control during the first two weeks, but damages were less in the third week. *Senna* demonstrated an inverse pattern compared with the control. Fertilizer lowered pod attacks in *Senna* during the first two weeks, but the steady increase in plots with NPK led to damages DAP 70 that were higher in *Senna* with fertilizer than without. The control reached its maximum at DAP 63 regardless of the NPK level. Damages in *Imperata* were lower at the beginning, when fertilizer was applied, but were higher one week later. At DAP 70, levels were similar.

Relative grain damage. The overall damage to grains reached 21.2^{d}%. Damages increased slightly over time from 20.7^{d} and 20.3^{d}% at DAPs 56 and 63, respectively, to 22.7^{d} at DAP 70. Significant differences between treatments were not suggested by analysis.

Estimated yield loss. Treatments had no significant impact on yield loss. Losses increased significantly from DAP 56 (3.0^{d}%) to 63 (7.0^{d}) and dropped slightly towards DAP 70 (6.3^{d}) ($F = 5.1^{*}$).

Fourth season (II/96)

Total pod numbers. Pod numbers were roughly doubled by fertilizer application across three weeks, DAPs 56, 63, and 70 ($F = 6.8^{*}$).

Total pod yield. Treatment impact was not recorded for total pod weight.

Pod weight. Pods were heaviest in the control, with 0.29 g per pod, compared with *Imperata* (0.24^{d}) and *Senna* (0.17^{d}). The difference between the control and *Senna* was significant ($F = 5.6^{*}$).

Relative pod damage. Mulch had a significant impact on pod attacks by the pod borer ($c^2 = 7.6^{*}$). *Senna* (0.8^{d}%) recorded lowest pod attacks, followed by the control (2.7^{d}) and *Imperata* (3.9^{d}); the latter was significantly different from *Senna*.

Relative grain damage. Significant variation was not revealed through treatments, the overall damage level was 24.5^{d}%.

Estimated yield loss. The estimated losses were very low and still resulted in zero when rounded to two digits after the decimal point. However, tentative analysis did not reveal significant differences.

Fifth season (I/97)

Total pod numbers. The application of NPK fertilizer led to a significant increase in pod production ($F = 11.6^{**}$). Among mulch treatments, plants in the control produced highest pod numbers and *Senna* lowest. This difference was significant ($F = 6.5^{**}$). *Imperata* was in between.

Total pod yield. Pod yields suggested a NPK*mulch*time interaction. Simple effects were used to solve this complex relationship. This turned out to be an effect on mulch treatments within non-fertilized plots. The control yielded higher results than *Senna* ($F = 9.6^{**}$). When plots received fertilizer, *Senna* was significantly lower in yields than *Imperata* and the control, which scored highest ($F = 6.0^{*}$). Mulch treatments also differed on trends ($F = 6.7^{**}$). The control started higher than mulch treatments at DAP 56, fell below the levels of *Imperata* at DAP 63, and reached highest yields again at DAP 70. *Senna* always remained at the lowest level.

Pod weight. Pods weighed 0.1^{d} g per pod at DAP 56 and increased to 0.3^{d} and 0.9^{d} during DAPs 63 and 70, respectively. Treatment influences were not suggested by analysis.

Relative pod damage. Overall damage to pods was significantly higher in fertilized plots, at 24.6^{d}%, compared with blank plots (23.0^{d}) ($c^2 = 8.8^{**}$). Mulch profiles revealed a different trend over the three sampling weeks on the first order polynomial ($c^2 = 13.7^{[l]**}$) (Table 5.14.). *Senna* showed a significant difference versus the control and *Imperata*. *Senna* started at DAP 56 with highest levels, peaked higher one week later, and dropped below the levels of the other two profiles at DAP 70.

Relative grain damage. Damage to grains did not suggest impact of treatments. The overall damage was calculated at 31.0^{d}%.

Estimated yield loss. Treatments did not significantly influence overall losses in pods. Losses rose from 1.7^{d}% at DAP 56 to 14.2^{d} and 6.2^{d} during DAPs 63 and 70. The increase to DAP 63 and its decline afterwards were significant ($F = 80.4^{**}$).

Lema

First season (I/95)

Total pod numbers. Mulch treatments were influenced differently over time. The control was significantly different from *Senna* and *Imperata* on the first order polynomial and *Senna* diverged in profile from *Imperata* on a quadratic trend ($F = 3.0^{*}$). The control had highest pod numbers at DAP 56 and DAP 63, and decreased constantly. It dropped slightly below levels of mulch at DAP 70. *Imperata* displayed higher pod numbers at the beginning and the end, in contrast with *Senna*. Whereas *Imperata* recorded a setback at DAP 63, *Senna* peaked during this sampling week and was higher in levels than *Imperata*.

Relative pod damage. Damages to pods were significantly higher in the control than in *Imperata* ($c^2 = 7.0^{*}$) (Table 5.15.). The control was separated from *Senna* on the first order polynomial ($c^2 = 14.5^{[l]**}$), and was the only treatment where early damage at DAP 56 was recorded. A slight peak occurred during DAP 63 and levels dropped thereafter. *Senna* displayed its first low attacks at DAP 63, but these increased steeply towards DAP 70. *Imperata*

rose constantly on comparatively low levels. However, damages at DAP 70 appeared in one replication only.

Relative grain damage. Incidences of pod attacks were rare and too few to be analyzed. However, among the few events, the lowest grain damage scores were about 12% and the highest close to 50%.

Estimated yield loss. No influence could be ascribed to treatments. At DAPs 56 and 63, percentages did not pass 0.2^{d}%. Since one replication recorded damages at DAP 70 only, analysis was not possible. A check of the raw data for the respective block revealed values close to 7.0^{d}%. However, this isolated event has to be regarded with caution.

Second season (II/95)

Total pod numbers. NPK fertilizer showed a significant impact on development of pod numbers over time (DAP) ($F = 5.3^{*}$). Without fertilizer, numbers increased constantly from DAP 49 until DAP 63, but when NPK was applied, comparatively higher numbers at the beginning decreased steadily. Pod numbers were comparatively low in total.

Relative pod damage. During three sampling weeks, only three events of pod attacks were noticed. They were all in the control, two times in fertilized and one time in non-fertilized plots. The rate was 1.3^{d}%. This was significantly higher than the zero levels in mulch ($c^2 = 6.7^{*}$).

Relative grain damage. During the three events of pod attacks in the control, attacks on grains ranged between 16.7 and 50% considering raw data. Analysis was not possible.

Estimated yield loss. Estimations were not possible on the basis of these rare incidences. Raw data showed that levels at DAP 49, which represented two of the three incidences, did not pass 0.03%.

Third season (I/96)

Total pod numbers. Significantly more pods were collected from fertilized plots ($F = 9.8^{**}$). However, a marginal NPK*mulch interaction suggested that in the control (with, without NPK) the levels were close together ($P \geq 0.05$).

Total pod yield. Pod yields increased constantly over DAPs 49-63 without a sign of significant variation among treatments.

Pod weight. Pod weights increased from DAP 49 (0.02^{d} g per pod) to DAP 56 (0.2^{d}) and DAP 63 (0.5^{d}). Apart from this time effect, treatments did not influence pod weight.

Relative pod damage. A complex three-way interaction was found ($c^2 = 16.2^{**}$). Simple effects were investigated for better understanding. Within non-fertilized plots, the control (linear trend) and *Imperata* (quadratic trend) together showed significant differences in profiles versus *Senna* ($c^2 = 20.1^{**}$) (Table 5.16.). The control and *Imperata* had no damages at DAP 49, whereas *Senna* already displayed attacks of 6.8^{d}%. *Senna* and *Imperata* peaked close to-

gether one week later, but the control revealed only about half the damage as the mulch. At DAP 63, mulch treatments dropped below those of the control. Within plots with NPK fertilizer, no significant variation occurred. However, the control and *Imperata* demonstrated almost congruent patterns whereas *Senna* remained about 10% lower during the peak at DAP 56. The basic response of mulch treatments to fertilizer levels was that the control with NPK exhibited highest damages but remained least attacked when no fertilizer was used. The inverse relationship between *Senna* and *Imperata* could be explained the same way. Because of a crossing of the profiles at DAP 63, the NPK effect was not valid generally. However, during the first two weeks, fertilized treatments recorded higher levels than blank plots.

Relative grain damage. A significant three-way interaction occurred for effects on grain damage ($c^2 = 18.8^{**}$). The analysis was split into simple effect for better explanation. Within non-fertilized treatments, the control and *Imperata* showed a significant interaction on the first order polynomial versus *Senna*. *Senna* remained stable during the three weeks (Table 5.17.). The control and *Imperata* showed no damaged grains at DAP 49, joined the level for *Senna* at DAP 56 and increased further towards DAP 63. Whereas *Imperata* increased only slightly, the control doubled its damage levels after DAP 56. When fertilizer was applied, no significant variation was found although the control increased to highest levels at DAP 63. The interaction in mulch on the two NPK levels can be seen mainly in the inverse profiles between the control and *Imperata* versus *Senna*.

Estimated yield loss. Fertilized plots (3.6^{d}%) always demonstrated higher yield losses than blank plots (1.4^{d}) ($F = 13.2^{**}$). The profiles for the two NPK levels also resulted in a significant variation on the quadratic trend ($F = 6.0^{[q]**}$). Without fertilizer, losses were comparatively low (0.2^{d}%) at DAP 49 and stabilized with 2.7^{d} and 2.1^{d} at DAPs 56 and 63, respectively. When plots received fertilizer, losses were already higher at DAP 49 (1.1^{d}) than without fertilizer; they peaked at DAP 56 (9.6^{d}) and decreased by about 75% to 2.3^{d} at DAP 63.

Fourth season (II/96)

Total pod numbers. The application of NPK fertilizer had a significant impact on pod formation and increased pod numbers more than threefold ($F = 21.2^{**}$).

Total pod yield. Similar to total pod numbers, fertilizer augmented pod yield more than four times ($F = 13.1^{**}$).

Pod weight. Weights per pod deviated among mulch treatments. They were significantly lighter in *Imperata* than in the control and *Senna* ($F = 9.9^{**}$) (Table 5.19.). The latter two did not vary significantly. Additionally, a trend indicated significant deviations between the profile of *Imperata* versus the control and *Senna* ($F = 6.5^{**}$). Pods in the control and *Senna* gained much faster in weight than those in *Imperata* and were generally more than two times heavier than in *Imperata*.

Relative pod damage. The three-way interaction between NPK, mulch, and time (DAP) was significant ($c^2 = 13.8^{**}$). For better understanding, this was split into simple effects within

fertilizer levels. Within non-fertilized plots, *Senna* was significantly different on the quadratic trend from *Imperata* mulch ($c^2 = 21.5^{**}$) (Table 5.20.). *Senna* had slightly higher levels at DAP 49, but remained low towards DAP 56 while *Imperata* rose to a distinct peak. *Imperata* dropped in damage at DAP 63 whereas *Senna* increased more than fivefold. The control increased towards DAP 56 and stabilized its levels for another week. Among the fertilized plots, *Imperata* revealed minor losses across time compared with the control and *Senna* ($c^2 = 10.5^{**}$). Trends were not significantly different in fertilized plots after ANOVAR. However, when using contrasts, a significant deviation of profiles of the control versus *Senna* ($c^2 = 4.6^{[l]*}$) and *Imperata* ($c^2 = 6.1^{[l]*}$) was suggested on the linear trend. The control started with higher damages than *Senna* and *Imperata* at DAP 49. Whereas *Senna* kept growing in damage levels much faster than the control during the three sampling weeks, *Imperata* increased slightly faster than the control during the first week. The control and *Imperata* recorded higher damages across time in fertilized plots ($c^2 = 8.0^{**}$).

Relative grain damage. NPK, mulch, and time (DAP) revealed a significant three-way interaction ($c^2 = 9.9^{*}$). For better understanding, the data set was split into simple effects. Assessing non-fertilized plots, the control was significantly different in profile from *Senna* on the linear trend and *Imperata* resulted in a significantly distinct trend on the second order polynomial versus the control and *Senna* ($c^2 = 20.0^{**}$) (Table 5.21.). *Senna* increased constantly over time, starting with damages below 5^{d}%. The control showed high damages at DAP 49 in contrast with both mulch types, displayed a setback one week later, and then increased again. *Imperata* had no damages at the beginning, rose to a maximum that was higher than the two other treatments, and fell below the levels of the control and *Senna* at DAP 63. The control had higher overall damage levels than *Senna* ($c^2 = 15.6^{**}$). On a marginal difference within fertilized plots, the control differed in trend from *Senna* ($P \geq 0.05$). The control started higher at DAP 49; *Senna* revealed about one-third of damages at that point but recorded higher damages the two following weeks.

Estimated yield loss. Yield loss was significant on the NPK*mulch*time interaction ($F = 3.1^{*}$). Again, the simple effects were used for better understanding. Within non-fertilized plots, *Senna* was significantly different in profile from the control and *Imperata* ($c^2 = 5.4^{**}$) (Table 5.22.). *Senna* started with levels close to zero (0.04^{d}%), increased to 0.8^{d} at DAP 56, and rose steeply to 13.0^{d}% above the levels for the control and *Imperata*. The losses in the control increased constantly and reached their maximum at DAP 63 (6.4^{d}). *Imperata* recorded no yield losses at DAP 49, peaked one week later with 5.2^{d}%, and dropped to 1.0^{d}% at DAP 63. Within fertilized plots, variation was not significant. However, *Senna* peaked highest at DAP 56 (16.3^{d}) and remained superior to all other treatments at DAP 63 (15.9^{d}). The control with NPK scored highest at DAP 49, with 2.3^{d}% estimated yield losses.

Fifth season (I/97)

Total pod numbers. Pod numbers reached different levels among NPK plots, showing higher values in non-fertilized plots ($F = 30.2^{**}$). They also changed differently on the linear trend. Whereas pod numbers without fertilizer increased from DAP 49 to DAP 56 and slightly set back towards DAP 63, their numbers constantly decreased from DAP 49 until DAP 63 in fertilized plots on a generally lower level than in non-fertilized plots ($F = 3.6^{*}$). Mulch showed impact on variation indicating significantly more pods in the control compared with mulch treatments *Senna* and *Imperata*, the latter without significant deviation ($F = 12.6^{**}$).

Total pod yield. Analysis was not possible. Treatments of mulch in combination with NPK fertilizer rarely revealed pods on which weights could be measured. If pods were present in fertilized or non-fertilized plots of mulch, they remained very small and underdeveloped and did not record any weight most of the time. The control almost always yielded pods. Although pod weight was relatively low, plants can be considered as having yielded at least a small number of pods.

Pod weight. Like total pod yield, the same particularities applied for pod weights. A consideration of these patterns showed that the pods for the control were slightly heavier but also underdeveloped. Variation was not significant.

Relative pod damage. Damages on pods deviated on trends among NPK and mulch levels (Tables 5.23a,b.). No fit could be obtained for the first and second order polynomials. However, the fertilized plots revealed higher damages at DAP 56 and dropped thereafter below the levels for non-fertilized plots ($c^2 = 6.6^{*}$) (Table 5.23a.). Both levels showed a weak set back at DAP 63. Comparing profiles of mulch, the control deviated significantly from *Senna* on a quadratic trend ($c^2 = 10.4^{*}$) (Table 5.23b.). Whereas the control had slightly less damage at DAP 56, damage levels in *Senna* fell one week later and increased again towards DAP 70. *Senna* started slightly higher than the control, decreased constantly, scored higher at DAP 63, and fell below levels of the control at DAP 70.

Relative grain damage. Because of the patchy data structure, no attempt was made to analyze grain damage.

Estimated yield loss. The many missing values for fertilized plots made it impossible to do a full comparison. An attempt was made to compare at least within non-fertilized plots. No differences were discovered.

IITA

First season (I/95)

Total pod numbers. Pod numbers did not differ significantly among treatments nor did they between sampling weeks.

Relative pod damage. Mulch profiles were significantly different on the quadratic trend ($c^2 = 18.8^{[q]**}$) (Table 5.24.). The control differed in trend from all mulch treatments. At DAP 56, the control revealed higher damage levels than *Senna* and neem, but was lower than *Imperata*. One week later, all mulch treatments scored higher than the control. This was the opposite at DAP 70, when the control showed slightly more damage. Among mulch treatments, *Imperata* recorded higher values than *Senna* and neem.

Relative grain damage. No significant impact occurred due to treatments. The overall damage level was 31.0^{d}%. Damages increased slightly over time with 29.1^{d}, 30.1^{d}, and 33.5^{d}% at DAPs 56, 63, and 70, respectively.

Estimated yield loss. Except for time effects, no variation could be ascribed to treatments. Yield losses decreased over time with 4.0^{d}% at DAP 56, 4.0^{d} at DAP 63, and 1.4^{d} at DAP 70. The drop from DAP 63 to DAP 70 was significant.

Second season (II/95)

Total pod numbers. Pod numbers did not vary significantly on treatment effects.

Relative pod damage. Some 492 pods were yielded during three sampling weeks across treatments and time. One was attacked at DAP 49, the eight remaining were damaged two weeks later at DAP 63. This corresponded with 1.8% overall on the raw data. Analysis was not carried out.

Relative grain damage. Because pod damage did not allow proper analysis, this was not tried for damaged grains either. From 3,094 grains in all attacked pods (raw data), 23.1% were damaged.

Estimated yield loss. Since one pod was attacked at DAP 49 only and no event was found at DAP 56, the sampling week of DAP 63 was investigated separately. No significant differences appeared. *Imperata* resulted in 1.1^{d}%, but the other treatments remained below 0.5^{d}%.

Third season (I/96)

Total pod numbers. Significant impact due to mulch treatments was not found.

Total pod yield. The same applied for pod yields, which constantly increased with time.

Pod weight. A significant variation occurred among mulch treatments, indicating that pods in the control were heavier than in all mulch treatments. *Senna* scored lowest, with pods that were significantly lighter than those in the control ($F = 4.8^{*}$). In general, pods weighed 0.03^{d} g per pod at DAP 56 and increased to 0.4^{d} one week later.

Relative pod damage. Mulch profiles could be separated between the control versus *Senna* and *Imperata* on a linear trend ($c^2 = 12.7^{[l]*}$) (Table 5.25.). The control already showed damage of 2.2^{d}% at DAP 49 when *Senna* and *Imperata* did not reveal pod attacks. DAP 56 indicated slightly less damage for *Senna* (9.1^{d}) compared with 12.4^{d}% for the control and

13.7[d]% for *Imperata*. At DAP 63, the control (29.5[d]) was more attacked than *Imperata* (22.5[d]) and *Senna* (21.8[d]). Neem showed 1.0[d]% attacked pods at the beginning and remained between *Senna* and *Imperata* during the following two weeks. However, the profiles were relatively close together.

Relative grain damage. Grain damages were not influenced by treatments. The overall damage on grains was 20.0[d]%, increasing from 4.2[d] at DAP 49 to 19.6[d] and 37.3[d] for DAPs 56 and 63, respectively.

Estimated yield loss. Yield losses were not significantly distinct among treatments. They increased from 0.04[d]% for DAP 49 to 2.1[d] and 8.6[d] for DAPs 56 and 63, respectively.

Fourth season (II/96)

Total pod numbers. Pod sampling took place at DAPs 56 and 63 and yielded relatively low numbers, which did not vary significantly among treatments.

Total pod yield. Pod yield was low and did not suggest any significant variation due to treatments.

Pod weight. Weights per pod were similar for the different treatments. Their weights were recorded with 0.25 g per pod at DAP 56, and there was a slight increase to 0.33 after one week.

Relative pod damage. Analysis of pod damage was not possible. Damage occurred during DAP 56 only and yielded five attacked pods out of an overall 737.

Relative grain damage. Analysis of grain damage was not attempted, either.

Estimated yield loss. Yield losses could not be compared between treatments. The overall estimate on the raw data remained below 0.4%.

Fifth season (I/97)

Total pod numbers. Pods could be sampled during DAPs 56 and 63. A significant interaction among mulch types was found between the two sampling weeks for *Imperata* versus *Senna* and neem ($F = 3.6^{*}$). *Imperata* was the only treatment where pod numbers increased from DAP 56 to DAP 63. The numbers decreased for the other treatments.

Total pod yield. Across both sampling weeks, the control yielded significantly lowest compared with the mulch types, which did not vary significantly among each other ($F = 4.4^{*}$).

Pod weight. Pod weights increased across treatments from 0.2 g per pod at DAP 56 to 0.8 g at DAP 63. Treatment effects were not discovered.

Relative pod damage. Mulch treatments revealed a significant difference, indicating that *Senna*, which yielded lowest pod attacks, was significantly less damaged than *Imperata* and neem ($c^2 = 11.8^{**}$) (Table 5.26.). Levels for the control remained between those of *Senna* and *Imperata*. The change of damage between the two sampling weeks was significant for neem

versus the control and *Senna* ($c^2 = 8.5^*$). The increase between the two sampling events was much stronger for the control and *Senna* than for neem.

Relative grain damage. Grain damage did not reveal significant variation when treatment differences were investigated. The overall damage rate was 27.4^d%.

Estimated yield loss. Treatments did not vary significantly at DAPs 56 and 63. Across treatments, the rate almost doubled from 2.4^d% to 4.3^d at DAPs 56 and 63.

Discussion

Regional differences

Relative pod and grain damage as well as estimated yield loss are the variables of major concern in this chapter. Although the results of total pod numbers, total pod yield, and pod weight are presented above, they are not discussed generally. Where considered necessary, these variables were used for explanation on damage patterns.

All regions

Relative pod damage. The differences between mulch treatments among regions were very weak in general (Table 5.4.). Lower pod damage in *Senna* treatments at IITA was a function of a comparatively lower larval abundance (Chapter 4) together with more pods leading to a slight reduction in attacks. Less pod damage in the control in Lema was ascribed in the same way to fewer larvae and more pods in these treatments. The control was barely more damaged in Tokpa/Ayou where slightly more larvae were recorded in parallel. However, these variations were of no biological importance.

Relative grain damage. Tokpa/Ayou recorded comparatively lowest damages on grains. Later instars leave flowers and bore into pods (Jerath 1968; Taylor 1978), where they complete their larval development. This is thus not a function of larval numbers in general but rather depends on how long the larvae feed within pods. The ratio of late to early instars was calculated from the data on parasitism in flowers (Chapter 4) that were obtained per region. This was valid since larval numbers were collected from the same 10 randomly selected plants per plot. These ratios were 1.1 for Tokpa/Ayou, 0.6 for Lema, and 1.2 for IITA (late/early instars). This indicates that late instars do not necessarily bore into pods but could stay in flowers until they reach their fourth or fifth instar. Tokpa/Ayou counted the highest flower numbers among the three regions (Chapter 2) and possibly offered the best source for prolonged flower feeding of later instars. They probably migrated into pods shortly before reaching the prepupal stage, thereby damaging only a small proportion of grains before they completely ceased feeding (Taylor 1978).

Estimated yield loss. Overall regional differences did not occur, but regions varied among each other in some seasons. IITA recorded highest losses ascribed to *M. vitrata* during season I/95. The estimator consists of relative pod and grain damage. IITA revealed more than threefold higher pod damage than Lema although the proportion of grains that was damaged, was one-third lower. Compared with Tokpa/Ayou, IITA showed higher damage levels on pods and grains within pods. During season II/96, Lema resulted in highest losses since by far the most pods as well as grains were attacked in this region. Tokpa/Ayou recorded the most elevated losses in season I/97. Pods were attacked most frequently and the highest proportion of grains was fed on in this region. Lema, which remained at lowest levels, resulted in least numbers of damaged pods and grains.

On-farm regions

Relative pod damage. Pod damage in Lema, which was more elevated in NPK plots during seasons I/95 and I/97, followed the larval abundance that was also higher in fertilized plots (Chapter 4). Fertilizer application slightly increased damage on pods in Tokpa/Ayou except for season I/96, when the rate remained roughly the same. Fertilized plots also recorded a slightly higher larval abundance, which probably accounted for more damage. However, the variation did not have biological relevance.

Relative grain damage. No evidence was found that more grains were fed on in fertilized plots across seasons and regions.

Estimated yield loss. Slightly higher yield losses in NPK plots were the result of tendentiously higher pod damage given no differences in grain damage. This was however too small to be of importance, however.

Seasonal differences within the same region

Tokpa/Ayou

Relative pod damage. More pods were damaged in all early seasons than in the late seasons; higher larval abundance in flowers and pods also prevailed in the early seasons (Chapter 4). Among early seasons, I/97 displayed by far the highest damages (Table 5.7a.) since larval numbers in pods were most elevated (Chapter 4) and, in turn, pod numbers were the lowest. This resulted in comparatively highest larval densities per pod with the consequence of higher damage. The comparatively higher precipitation in season I/97 favored the abundance of *M. vitrata* as adults' emergence from the pupa is promoted by rainfall and soil humidity (Kranz et al. 1979). Although season I/95 yielded fewer larvae per 10 plants, damages were still higher

than in I/96. This probably was compensated for by fewer pods in season I/95, which increased larval densities leading to more damage.

In contrast to Taylor (1967), who found that damage on pods generally is higher in the late seasons due to an accumulation in larval population (Taylor 1978), the present study revealed highest damage in early seasons. This can be explained by significantly higher thrips numbers during late seasons, which greatly limit the access to flowers by *M. vitrata* due to high damage (Taylor 1967; Jackai & Singh 1991). The larval population in cowpea flowers is thus reduced in late seasons, resulting in less damage although the population in fact is accumulating during the year (Summerfield et al. 1974; Taylor 1978). In seasons I/95, II/96, and I/97 pod damages were higher in fertilized plots (Table 5.7a.) together with increased larval abundance in pods in NPK plots (Chapter 4). Although pod numbers increased in fertilized plots, too, the factor by which they increased from non-fertilized plots to fertilized ones was smaller than the factor by which larval numbers increased between NPK levels. The population in fertilized treatments thus became denser in these plots. This explains the higher damage.

The decrease in pod damage in season II/95 after fertilizer application was due to higher pod numbers combined with lower larval abundance in pods (Chapter 4). A distribution effect occurred that could have reduced damage. Season I/96 remained almost stable. The slight reduction in NPK plots was considered not important. Pods were slightly more damaged in *Imperata* mulch during seasons I/95 and II/96 compared with the control. This happened together with higher larval abundance in *Imperata,* too, accounting for increased damage. Pod numbers were almost the same in both treatments, indicating that larval densities increased in *Imperata*. The control revealed highest damages in seasons II/95, I/96, and I/97, where also more larvae were counted in pods (Chapter 4). *Imperata* mulch recorded higher damages than the other treatments in seasons I/95 and II/96. Larval abundance in *Imperata* was also higher in season II/96, accounting for more losses. *Imperata* mulch had higher larval numbers in season I/95 than the control, but larval abundance in *Senna* was more elevated than in *Imperata*. However, since *Imperata* counted fewer pods than *Senna,* larval densities were higher in *Imperata,* thus leading to higher damages of pods.

Relative grain damage. Seasons I/97 and II/95 showed a higher proportion of infested grains than II/96, I/95, and I/96. Season I/97 recorded by far the highest larval numbers (Chapter 4) and also more pods per 10 plants of each plot. Since larval densities in these plots (larvae per number of harvested pods) were also much higher, these high damages could be explained. Thus, probably more than one larva contributed to the damage per pod, the individual damage of which Taylor (1967) estimates between 10 and 20%. As for season II/95, very few pods and larvae were found but damage to grains was the highest. The weight per pod during the late season II/96 was lower than for seasons I/96 and I/97, both early seasons, indicating that the pods in the late season were less developed and thus contained fewer grains per pod, as generally observed. The damage to the total fewer grains probably resulted in the relatively higher damage scores. Pod weights were taken starting with season I/96 but did not allow an estimate

for pods during this season. The remaining seasons yielded fewer larvae in high pod numbers. Hence, larval densities per pod were lower, accounting for reduced attacks on grains.

Estimated yield loss. Yield losses were distinct between early and late seasons. Early seasons recorded higher pod attacks, whereas grain damage did not vary considerably between early and late seasons except for season II/95. However, the generally low damage rate of pods in this season put relatively less weight on the comparatively higher grain damage. Since larval abundance was generally more elevated in flowers in early seasons (Chapter 3), a higher pressure on pods by late instars was to be expected.

Lema

Relative pod damage. Seasons II/96 and I/96 scored highest in terms of pod damage, whereas II/96 was also higher in damage rates than I/96. Season II/96 recorded the highest larval number per pod (density), followed by I/96. These density differences could be explained by 0.7 times fewer larvae but half of the number of pods harvested in season II/96 compared with I/96. Hence, densities were higher in season II/96, leading to more damage in pods.

Relative grain damage. The control yielded less grain damage than the mulch treatments during seasons I/95 and I/97, while in parallel more pods were obtained from mulch. Since larval abundance between treatments did not vary considerably, larval densities in mulch treatments were higher. This probably led to incidences where more than one larva fed inside a pod, increasing the damage to grains. Seasons I/96 and II/96 resulted in more grain damage in the control than in mulch treatments. As for season I/96, the control counted slightly fewer pods but the larval densities did not reveal important variation among treatments. Rather, the ratio of late to early instars was most elevated in the control. Since later instars are known as to be more voracious (Taylor 1967), their higher consumption of tissue might be a reason for more grains being damaged. Higher larval numbers collected from infested pods possibly accounted for the higher grain damage in season II/96 in the control. Since the total number of collected larvae was more elevated than the overall pod numbers, more than one larva per pod was likely to inflict grain damage.

Estimated yield loss. Seasons I/96 and II/96 displayed highest yield losses, which were higher than in season I/97, but all three seasons recorded higher losses than I/95, II/95, and I/97. This was a function of larval numbers obtained from pods (Chapter 4) and number of pods harvested, which yielded highest densities in season I/96, followed by II/96 and I/97.

IITA

Relative pod damage. *Senna* mulch recorded about 2 and 3% less damage compared with the control and *Imperata*, respectively. *Imperata* yielded more larvae out of pods, with a higher ratio of late to early instars. The higher larval abundance in *Imperata* together with a

higher proportion of late larvae, which are more voracious than earlier instars (Taylor 1967), is likely to explain the difference in damage to the control. As for the control, differences in pod numbers as well as larval numbers obtained from pods compared with the *Senna* treatment did not allow conclusions on the variation. The addition of data on larval numbers in flowers (Chapter 3) disclosed a tendency towards slightly more larvae in flowers in the control compared with *Senna*. However, the variation between the three treatments was of no biological importance.

Relative grain damage. Although no significant variation was found among treatments or seasons, the control showed a lower proportion of damaged grains. Analysis of larvae obtained from pods, and the number of collected pods, showed that larval densities were slightly reduced in the control and that there was a lower ratio of late to early larvae. This indicates less larval pressure as well as a relatively lower amount of grain tissue consumed (Taylor 1967).

Estimated yield loss. Since estimated yield loss was calculated differently compared with grain damage, both late seasons (II/95, II/96) could be included in the analysis but recorded levels were close to zero. First cropping seasons reported significantly higher losses due to basically more pod damage and more cases of grain damage. Considerably low precipitation in both late seasons (Table 2.6.) did not favor a large population of *M. vitrata.* In general, larval abundance in cowpea was significantly higher in early seasons (Chapter 3) and thus accounted for higher damage to pods.

Differences within seasons

Tokpa/Ayou

First season (I/95)

Relative pod damage. Differences between NPK levels occurred in *Senna* and *Imperata*. Higher damage in *Senna* without NPK can be explained by larger numbers of larvae (Chapter 4), which were collected in fewer total pods thus increasing the larval density. In *Imperata* mulch this was the opposite. Higher damage was observed in fertilized plots where more larvae were encountered in overall fewer pods. The larval density was increased, too. Considering the trend on NPK levels, fertilized treatments showed higher damage at DAPs 56 and 63 but dropped below the levels of non-fertilized plots at DAP 70. Slightly higher pod numbers and more larvae in fertilized plots revealed higher densities in these plots during DAPs 56 and 63, but a drop in larval numbers in the same plots at DAP 70 below the levels for non-fertilized plots led to comparatively lower densities in fertilized treatments. In parallel, slightly higher flower numbers at DAP 56 in NPK plots also attracted more larvae. This was probably

the effect of NPK, which increased flower numbers and the nutritive quality for larvae, and was probably more attractive for ovipositing adults (Bentz et al. 1996). The trend, which indicated that damage levels grew faster over time in non-fertilized plots, was also recognized in flower numbers (Chapter 2) and larval abundance in flowers (Chapter 3). NPK application probably attracted larvae earlier, but faster senescence in these plants (Wien & Tayo 1979; Wien & Summerfield 1984) resulted in faster decrease in oviposition and faster pod ripening. Pods thus were abandoned more quickly as their nutritional quality deteriorated.

Relative grain damage. Treatment differences did not occur. Grain damage increased over time from DAP 56 to DAP 63 and dropped thereafter. In parallel, most larvae were encountered at DAP 63 (Chapter 4), which was the peak in grain damage. As pods grow older, their suitability generally decreases through ripening thus causing larvae to leave.

Estimated yield loss. Yield losses over time peaked at DAP 63. Attacks of pods and grain damage showed the same patterns over time and hence led to this peak.

Second season (II/95)

Relative pod damage. The underlying effect was attributable to the fact that *Senna* showed no damaged pods in non-fertilized plots but was the only treatment with attacks in fertilized plots at DAP 70. However, pod numbers were very low in this season and larvae were rarely encountered. Within non-fertilized plots, the control had 2.4 pods out of 26.3 damaged, and 1 pod out of 13.7 in *Imperata* showed signs of attack. In *Senna* with NPK application 0.8 pods were attacked in a total of 26 pods. These results were ascribed to chance.

Relative grain damage. Very few damaged pods were encountered out of overall low pod numbers. More larvae were counted in flowers of fertilized treatments (Chapter 3) and they accounted for relatively more damage to grains as they moved into pods during their development.

Estimated yield loss. According to findings for damaged pods, yield losses showed the same patterns. The small differences of not more than 1% between treatments on the background of overall few damaged pods were considered biologically insignificant.

Third season (I/96)

Relative pod damage. The basic characteristic of the underlying three-way interaction was, on the one hand, the difference in profiles of the control to both mulch treatments. On the other hand, profiles for the control had a different onset at DAP 56 due to NPK application. Also, both mulch treatments showed inverse levels due to use of fertilizer. Numbers of larvae, which were collected in pods (Chapter 4), reflected the same patterns and were the main reason for variation in pod damage. High damage was accompanied by higher larval abundance in pods.

Relative grain damage. Treatment differences were not observed. Damage scores remained stable at DAPs 56 and 63, but rose by about 2% towards DAP 70. Increases in pod

numbers, which still occurred after DAP 63, indicated that the physiological ripening of pods was delayed. More than 60 mm precipitation was recorded between DAPs 63 and 70 principally contributing to this delay. Hence, pods were still suitable for feeding of late instars. This prolonged feeding might explain the again increasing damage to grains.

Estimated yield loss. Losses increased from DAP 56 to DAP 63 but slightly decreased towards DAP 70. Relative pod damage decreased after DAP 63 as well. The newly set pods at this late stage increased the total number of pods and thus relatively reduced damage rates. This effect was stronger than rising grain damage as the decreasing yield losses indicated.

Fourth season (II/96)

Relative pod damage. The differences in damage can be explained with the corresponding numbers of larvae collected in pods (Chapter 4). Numbers were highest in *Imperata* and lowest in *Senna*. Taking into account the larval abundance in flowers (Chapter 3), they followed the same patterns as was recorded for pods. Since larvae move from flowers into pods as they mature (Taylor 1978), their abundance in pods is likely to follow those recorded in flowers.

Relative grain damage and estimated yield loss. Since relative grain damage did not vary significantly and the differences in pod damage among treatments were fairly small, yield losses were not distinct.

Fifth season (I/97)

Relative pod damage. Pod numbers were always lower in *Senna* than in both other treatments. Larval abundance in pods was higher in *Senna* compared with the control and *Imperata* (Chapter 4). *Senna* thus resulted in highest larval densities per pod leading to comparatively higher damage. Since the increase in pod numbers over time was slowest for *Senna*, the "dilution effect" by newly set pods was slower than for the other treatments. This continued until DAP 63, when larval numbers grew more slowly in *Senna*. The larval densities per pod in *Senna* dropped accordingly. More pods were damaged in the control and *Imperata* after DAP 63 as larval numbers were higher at DAP 63 in both treatments.

Relative grain damage and estimated yield loss. Grain damage did not vary among treatments but the peak in yield loss at DAP 63 was ascribed to the maximum in larval abundance in pods (Chapter 4).

Lema

First season (I/95)

Relative pod damage. Overall pod numbers were low in this season and decreased in numbers for the control and *Senna* from DAP 56 to DAP 70. Higher total larval numbers in flowers (Chapter 3) for *Senna* but many fewer pods compared with the control resulted in more larvae moving into fewer pods in *Senna*. Almost no larvae were found in pods due to the insufficient development of pod size. The strong increase in damage in *Senna* compared with the control and *Imperata* needs to be seen in relation to low pod numbers, the difference between treatments thus appearing unimportant. However, damages at DAP 70 occurred in one replication only. This suggests a strong bias of results, which cannot be explained by the particular site conditions.

Relative grain damage and estimated yield loss. The fact that pods generally were very small led to comparatively high grain damage in rare cases, which cannot be considered representative. Yield losses remained at low levels and the isolated events at DAP 70 in one replication cannot be accounted for, either.

Second season (II/95)

Relative pod damage. Low pod numbers were counted in this season. Larval abundance in flowers (Chapter 3) also remained at low levels for the three treatments. Except for one larva, which was encountered in *Imperata*, all the other few specimens that accounted for cases of damage were collected in the control.

Relative grain damage and estimated yield loss. Due to small pods with underdeveloped and therefore small grains, the three events of attack led to relatively high grain damage, which, however, cannot be considered representative. Because the total pod number was low, the isolated events did not cause losses worth mentioning.

Third season (I/96)

Relative pod damage. The differences in trend between *Senna* mulch versus the control and *Imperata* in non-fertilized plots basically consisted of the events of damage at DAP 49 in *Senna*, where both other treatments did not show attacked pods. Given similar numbers of larvae in pods (Chapter 4), the densities were higher in *Senna* at DAP 49 due to lowest pod numbers therefore increasing the probability of damage. The control had lowest damage at DAP 56 compared with both mulch treatments although larval abundance was slightly higher at this time. However, pod numbers were higher in the control during the first two sampling weeks (DAPs 49, 56) and larval abundance in flowers was lowest overall (Fig. 3.8.) (Chapter 3), indicating that the migration pressure from flowers to pods was expected to be lowest in the control and to result in reduced damage. The basics of the interaction, which indicate that

the control without fertilizer resulted in lowest damage but revealed highest attacks when fertilizer was applied, can be explained using the pod numbers per treatment in combination with the expected larval pressure shifting from flowers to pods. Without fertilizer, pod numbers were highest but larval numbers in flowers were lowest. After fertilizer application, the opposite was the case, with lowest pod counts but highest larval numbers in flowers. Damage to pods was higher during DAPs 49 and 56 in NPK plots due to many more larvae collected from fertilized treatments. Together with only slightly more pods in these plots, the larval density per pod was remarkably higher, therefore causing more damage.

Relative grain damage. The damage patterns on grains followed straightforward those for pod damage due to the respective larval numbers, as larvae are likely to cause more overall damage to grains when they are more abundant.

Estimated yield loss. As was observed for damage to pods, yield losses were higher in fertilized plots during DAPs 49 and 56, accounting for the respective patterns of pod damage and subsequent grain damage.

Fourth season (II/96)

Relative pod damage. The mulch treatments *Senna* and *Imperata* showed distinctly different quadratic trends within non-fertilized plots, which only partially found expression in pod and larval numbers. The decrease of damage after the peak at DAP 56 for *Imperata* was caused by a sudden increase in pod numbers in parallel, which subsequently "diluted" the damage while larval numbers in pods rose more slowly (Chapter 4). Pod numbers in *Senna* remained stable during three weeks and no larvae were encountered in pods. The increase in damage after DAP 56 can probably be attributed to larvae that fed on pods but left before the next sampling took place. Since sampling was done weekly, instars three, four, and five together would have needed seven days at maximum (Taylor 1967; Vishakantaiah & Jagadeesh Babu 1980) to complete their cycle. In the fertilized plots, the lowest damage in *Imperata* compared with the control and *Senna* was a function of overall slightly lowest larval numbers.

Relative grain damage. Grain damage followed principally the same patterns over time and among treatments as the damage to pods, which is a function of larval and pod numbers. As an exception, grain damage in the control dropped at DAP 56 whereas it rose for both other treatments. Faster gain in pod weight in the control between DAPs 49 and 56 probably compensated for losses. Pod weight is positively correlated with number of seeds per pod, weight per seed, and pod length (Rachie & Roberts 1974), suggesting that the faster increase in pod weight in the control plants led to a "dilution" of grain damage since larval numbers in pods (Chapter 4) rose slowly in parallel.

Estimated yield loss. As a function of pod and grain damage, yield losses followed the patterns in damage, which were similar for pods and grains.

Fifth season (I/97)

Relative pod damage. Many treatments did not yield pods during this season, which made analysis very difficult and strongly biased. Those from which pods were collected, yielded extremely small pods, which did not have any measurable weight. The small mean differences together with many missing values did not allow sound interpretation.

Relative grain damage and estimated yield loss. Because of the very small pods, where the number of grains often could not be estimated, grain damage could not be assessed. However, since few pods were harvested throughout the season, considerable losses must have occurred in the flower stage, at which time damage is principally ascribed to thrips. Losses due to *M. vitrata* were infinitely small and can be entirely neglected.

IITA

First season (I/95)

Relative pod damage. The control decreased steadily in damage whereas mulch treatments had a peak damage at DAP 63. This could be explained by lowest larval numbers in pods during the first two sampling weeks (Chapter 4) and increasing pod numbers leading to lowest larval densities per pod. *Imperata* had highest damages as pod numbers remained lowest and larval abundance was comparatively high.

Relative grain damage. Grain damage did not differ among treatments but damage rose slightly over the three weeks, as larvae feed in pods and become increasingly voracious as they grow (Taylor 1978).

Estimated yield loss. Yield loss decreased over time as more pods were developed and pods ripened, thereby losing suitability for larvae. As larval abundance in flowers dropped close to zero at DAP 63 (Fig. 3.11.) (Chapter 3), the population decreased and late instars left pods for pupation (Taylor 1967).

Second season (II/95)

Relative pod damage, relative grain damage, and estimated yield loss. No treatment differences occurred during this relatively dry season. Low larval abundance in flowers (Fig. 3.12.) (Chapter 3) indicated conditions that were not favorable for *M. vitrata* and thus resulted in very little damage and hence yield loss.

Third season (I/96)

Relative pod damage. The control showed slightly increasing damage levels between DAPs 56 and 63 in contrast to the other treatments. This was the only treatment where pod numbers decreased after DAP 56, which can be explained as a concentration effect of larvae in

pods. Since flowers in the control yielded highest larval counts during two weeks (DAPs 49, 56) (Fig. 3.13.) (Chapter 3), a higher pressure can be assumed on pods, where late instars complete their larval development (Taylor 1967).

Relative grain damage. Treatment differences were not observed but damage to grains increased considerably during the three weeks. Highest precipitation was recorded in this season among all others, which delayed the ripening process of pods. The suitability thus was prolonged, leading to continued feeding on pods. This was confirmed by a decreasing ratio of late to early instars from 26 to 19 for DAP 56 and DAP 63, respectively, indicating that a new larval generation started feeding on pods, too.

Estimated yield loss. Yield losses increased over time as a function of increasing pod and grain damage. Their level of 8% at DAP 63 was considered low.

Fourth season (II/96)

Relative pod damage, relative grain damage, and estimated yield loss. Treatments did not differ in this season. Precipitation remained below 100 mm (Table 2.6.) thus causing water stress, which was confirmed by smallest plants in relation to all other seasons (Table 2.8.) (Chapter 2). The flower set remained lowest, too (Table 2.9.). These were unfavorable conditions for *M. vitrata*, which resulted in rare attacks on pods and caused very little grain damage. Yield loss thus remained close to zero.

Fifth season (I/97)

Relative pod damage. *Senna* mulch yielded lowest damage levels, which were mainly induced through highest pod numbers (together with neem) and comparatively low larval abundance in pods (Chapter 4), thus showing low larval densities per pod. Since larval abundance (Chapter 3) in flowers was low, too, the migratory pressure of aging larvae was reduced. Neem mulch differed on the trend from the control and *Senna* mulch due to its higher damage levels at DAP 56. These were a function of only slightly higher pod numbers and by far highest larval abundance in pods. Larval densities were higher in total (across time) and thus caused more damage on pods. Larval abundance in flowers was higher in neem at DAPs 49 and 56 (Fig. 3.15.) (Chapter 3), leading to a higher migratory pressure from flowers to pods as larvae grew.

Relative grain damage and estimated yield loss. Neither grain damage nor yield loss varied significantly among treatments and overall yield losses were considered low.

Conclusions

The attempt to assess damage to pods and grains as well as to estimate the yield loss due to an isolated pest is difficult, since that pest competes with other pre-flower and flower (e.g., *M. sjostedti*) as well as post-flowering pests (e.g., *Apion varium*, pod sucking bugs) (Dreyer &

Baumgärtner 1995). Flower thrips occur very early on plants and lead to damage that can completely bias subsequent attacks while masking the real importance of pests relying on organs that appear later, e.g., pods. For precise investigations on the real damage per pest, it would be indispensable to consider the impact of competition within the pest complex on each single pest. It was not the scope of this study to work out the real potential of damage by *M. vitrata*, rather, the focus was the comparison of damage and losses among treatments. No attempt was made to adjust for treatment influences that might have biased the pest complex differently due to alleged preferences of every single pest species. Thus, the results are regarded as a rough estimator for damage patterns ascribed to *M. vitrata* and should assist in explaining the various possible components that may lead to these damages.

Across all regions and seasons, damage by *M. vitrata* was never considered important, in either flowers (Chapter 2) or pods as indicated by the estimated yield loss variable. The basic factor was believed to be the flower thrips (Chapter 3), which supposedly masked the potential importance of the pod borer (Jackai & Singh 1991). Pod damage could be explained in most cases by the relation of larval abundance in pods to the respective pod numbers, which allowed the calculation of larval densities per given number of pods. More damage came about by higher larval densities in pods.

Larval abundance in flowers was also considered. Numbers of larvae in flowers are likely to be at the origin of pod attacks, since they do not wander around much to reach pods for completion of their larval development (Taylor 1978). A model created by Odulaja & Oghiakhe (1993) considered the parameters flower infestation and larval abundance as most suitably describing yield loss in cowpea. Cases were observed during the current study, particularly in Lema, where late instars were encountered in flowers thus not accounting for pod damage. Since overall few and mostly underdeveloped pods prevailed in this region, their suitability in terms of size was regarded as a limiting factor for late instars. It is likely that the lack of appropriate requirements of pods explained continued feeding in flowers, thereby proving that pods are not necessary for the completion of the life cycle of *M. vitrata*.

The relationship between larval abundance and pod numbers also explained grain damage. Depending on the larval density per given number of pods, more than one larva per pod was encountered hence accounting for increased pod damage, which is estimated between 10 and 20% per individual larva (Taylor 1967). Precipitation influenced pod ripening and thus affected the suitability of tissue for feeding larvae. Continuing rainfall towards the end of the season delayed the ripening process and allowed prolonged feeding of larvae. In cases where rainfall continued, which happened in early cropping seasons, early instars were encountered in pods. This indicated a new generation that basically relied on pods due to scarcity of flowers towards the end of the season. Grain damage was increased thereby. The relationship between pod weight and number of seeds or pod length (Rachie & Roberts 1974; Karel & Mghogho 1985) offers an additional tool for explaining grain damage. Damage is expected to be rela-

tively higher the smaller pods are (i.e., shorter pods, fewer grains, smaller grains) since feeding larvae proceed faster in relation to pod size.

Estimated yield loss was a multiplier constructed from attacked pods and damaged grains ascribed to *M. vitrata*. All factors that accounted for both measures separately entered this estimator, too. Among both arguments of the multiplier (number of damaged pods, number of damaged grains per pod), the first was found to be the stronger influence on differences in yield losses between treatments. Larval abundance, which was the major factor of influence during this study, has direct consequences on the number of probed pods but to a lesser extent determines the number of grains damaged, where measures like larval age, pod size, and pod age join in.

Direct treatment effects from mulch or NPK fertilizer did not occur and have to be regarded as indirect causes that influenced plant growth (Chapter 2) and pest populations (Chapter 3).

6 Cowpea yields as influenced by mulch application and use of NPK fertilizer: The difficulty in accounting for influences of insect prevalence

ABSTRACT Grain legumes are known for unreliable seed yields in spite of their high yield potential. The variability was confirmed by several studies from literature on cowpea, *Vigna unguiculata* (L.) Walp. (Leguminosae). Several factors are suggested in this study as principally influencing final yield, such as pest abundance, soil properties, climate, flower numbers per plant, pod numbers per plant, pod weight and seed number per pod. Plants were harvested when more than two-thirds of pods were ripe, with 50 plants chosen randomly per plot and harvested entirely. Pods were dried, weighed, counted, and husked and grains were weighed again for final grain yields. Mixed models ANOVA was applied for statistical assessment. Flower numbers per plant were considered the basic measure for determining cowpea yield. Pest abundance, soil properties, and natural flower shedding were suggested as the main factors that further define the number of pods that are finally set given the initial number of flowers. Interactions of these factors made it difficult to judge their individual importance. Pests were identified as the most important cause of yield reduction or failure. Whereas NPK led to vegetative overgrowth of the plants, thus greatly reducing the onset of reproductive organs, it was also found to improve plants' vigor and enabled them to tolerate higher thrips abundance. Mulch did not exert influences on any of these measures. Although pest damage is among the most important causes of considerable yield loss in cowpea, its dimension is difficult to extrapolate.

Grain legumes are noted for their relatively low and unreliable seed yields in relation to their undoubtedly high yield potential (Summerfield et al. 1978). The range within which cowpea yields were reported is enormous. On the lower end, Slade (1977) measured 88 kg per hectare on the average for West Africa, while 224 kg per hectare or less were reported by Ezedinma (1960), Ebong (1965) and Ojehomon (1970) in Nigeria. Summerfield & Roberts (1983) described yields between 1,000 and 2,800 kg per hectare in the USA, and over 4,000 kg per hectare were reported by Nangju et al. (1977) from Ethiopia. In controlled environments, seed yield was found to depend on the number of pods reaching maturity (Summerfield et al. 1978); this was confirmed by Littleton et al. (1979b), who noted that there was a strong relationship between final pod number and total plant dry weight. For the determinate growth type, Wien & Summerfield (1984) stated that plant growth (number of nodes) at flowering might have important consequences for subsequent economic yield, but for indeterminate types, the effect was very small. Summerfield et al. (1983) summarized that the so-called phenological potential is equivalent to the number of reproductive nodes plus associated changes in the total number

of flowers and has large effects on economic yield. Janoria & Ali (1970) explained 83% of variation in yield with three factors: pod number per plant, seeds per pod, and seed weight.

One basic cause of low cowpea yields is damage by pests, the two most damaging of which are *Maruca vitrata* and *Megalurothrips sjostedti* (Taylor 1964; Singh & van Emden 1979; van de Klashorst & Tamò 1995). Through effective chemical pest control, yields can be increased dramatically, showing the important damage caused in cowpea through pests (Muller & Sellshop 1954; Booker 1965; Ebong 1965; Ojehomon 1970; Cardona & Karel 1990; Afun et al. 1991; Jackai, pers. comm.). Muller & Sellshop (1954) and Ebong (1965) increased yields of local cowpea varieties from 224 kg to 1,778 kg per hectare in South Africa and Nigeria through successful pest control alone. Booker (1965) and Ojehomon (1970) suggested that effective pest control increased cowpea yields much more than fertilizer application or selection by breeding.

The second concern is the number of flowers that are dropped naturally. Rachie & Roberts (1974) estimated a natural flower shedding of up to 88%. Including additional losses of premature pods, they calculated that only 6-16% of initially set flower buds produce mature pods. These results were basically confirmed by Wien & Summerfield (1984), who estimated that 9-18% of flowers produce mature fruits. The proportion of “useful” or “useless” flowers, which contribute or do not contribute to fruit production (Ojehomon 1968), thus represents a huge waste of resources and might partly contribute to the wide ranges in cowpea yields. The underlying mechanisms or reasons are as yet not fully understood and Ojehomon (1968) proposed three hypothesis for flower shedding: 1) early flowers monopolize nutrients and starve younger ones; 2) older flowers produce inhibitory substances, which stop the development of younger flowers; and 3) pollination/fertilization is unsuccessful for younger flowers. The first hypothesis was confirmed by Summerfield et al. (1983), who proposed that older flowers received more assimilates to the detriment of younger ones. It seems therefore extremely difficult to estimate cowpea yields as both complexes, the pest problem and natural flower shedding, are very likely to interact with soil conditions and climate. This study aimed to clarify how far cowpea yields could be explained by assessing preceding pest abundance throughout the flowering period.

Materials and Methods

At the end of each growing season, all plots were harvested to assess the extent to which yield could be explained through preceding abundance and damage by the two pests. All plots were harvested simultaneously within the same region. The crop normally ripens unevenly, which makes its time for harvesting difficult to determine. A common standard was thus applied: harvesting when more than two-third of the pods were ripe (Duke 1990). This turned out to be a convenient measure to attain almost maximum possible yields without losing too many of the small and underdeveloped pods, which started falling off when they were ripe.

Under often humid conditions, at the end of early rainy seasons in particular, pods started rotting and lost weight rapidly. The use of this approach prevented the inclusion of too many young pods of the second cycle. There were often differences in harvesting dates by one or two weeks among regions but most were at DAP 70 or DAP 77. In all first growing seasons in particular, it was difficult to obtain uniformity due to the semi-determinate habit of the variety used, whereas the second seasons were much more homogeneous due to early suspended rains.

Fifty randomly chosen plants per plot were harvested entirely, including small pods that originated from the second flowering generation. All plants that had already been marked for phenological studies, for weekly harvest for parasitization studies in pods, or for studies on damage, were left out. All pods per treatment were put into envelopes (45 x 20.5 cm/25g – length x width/weight) and brought to the laboratory. They were counted and put in the oven (80°C for 96 hours or 105°C for 72 hours). Afterwards, the pods were weighed for dry matter and husked; grains were then returned to the oven for 24 hours to be weighed thereafter for dry matter grain yield. In addition, weights per pod were calculated. Investigations were limited to pod numbers, seeds per attacked pods, seed yield, and weight per pod, which account for about 83% of variation in yield (Janoria & Ali 1970; Littleton et al. 1979b). The yields per hectare (in kg per hectare) were obtained by dividing the means of yield by 50 and multiplying it by the corresponding extrapolated plant number per hectare. This resulted from the calculated plant numbers per plot and was achieved by multiplication of plant numbers within row by number of rows given the size of each plot.

After assessing normality and variance structure on the standardized residuals, ANOVA for mixed models in SAS was carried out. If necessary, data were $\sqrt{(x + {}^{3}/_{8})}$ transformed before analysis. Mean scores of 50 plants per plot were used as responses for total pod numbers, weight per pod, and dry matter yield of pods and grains. After each ANOVA, least squares means were conducted for separation of means. To account for *a priori* chosen treatment differences, orthogonal contrasts were selected. Since contrasts can represent combinations of comparisons as "weighted sum of means" (Hand & Taylor 1987, p. 10), they were used to compare different clusters, e.g., first growing seasons (I/95, I/96, I/97) against second growing seasons (II/95, II/96), or no mulch (control) versus mulch ([*Senna siamea* (called *Senna*) + *Imperata cylindrica* (called *Imperata*)]/2).

To distinguish seasonal and regional patterns, seasons and regions were incorporated as additional factors. For comparisons between regions and between seasons within regions, replications were nested within region and season, respectively, to use a hierarchical error term (Korie, pers. comm.).

A *P*-value of 0.05 was generally used to judge significance, although higher levels were considered as marginal responses if reckoned important. *F*-values were marked with one star (*) if $0.05 > P \geq 0.01$ and with two stars (**) if $P < 0.01$.

The exact description of experimental sites and the research design, auxiliary data like climate and soil properties, and a detailed description of the statistical approach were discussed completely in Chapter 1.

Results

Regional differences

NPK was not used at IITA. Hence, regional differences were tested in two steps. An overall comparison of the three regions did not consider NPK, leaving mulch as the single treatment factor. The neem treatment at IITA was excluded as well, because it was a special component for the on-station trials only. A second step compared the two on-farm regions Tokpa/Ayou and Lema, controlling for NPK.

All regions

Total pod numbers. Counting or pod numbers per treatment was started with season II/95. Overall pod numbers harvested across treatments and seasons were significantly higher at Tokpa/Ayou than at IITA and in Lema ($F = 16.5^{**}$) (Table 6.1.). A comparison of seasons across regions indicated that pod numbers were significantly higher in early growing seasons (I/96, I/97) than late seasons (II/95, II/96) with the exception of Lema between seasons II/96 and I/97, where the opposite effect occurred ($F = 81.6^{**}$). In some seasons, pod numbers were different among regions. Counts did not differ significantly in seasons II/95 and II/96. Within season I/96, Tokpa/Ayou recorded significantly higher numbers than both other regions, which were close together. At the end of season I/97, Lema scored significantly less than IITA and Tokpa/Ayou. This interaction was significant ($F = 5.2^{**}$).

Pod weight. Regions interacted significantly with seasons ($F = 22.2^{**}$) (Table 6.2.). At the end of season II/95, IITA yielded the significantly heaviest pods compared with Tokpa/Ayou and Lema, whereas season I/96 significantly favored Tokpa/Ayou over Lema and IITA. In turn, Tokpa/Ayou recorded the lightest pods in season II/96. This was significantly less than in Lema and at IITA. Lema scored significantly lowest for season I/97 when compared with IITA and Tokpa/Ayou. Pods were significantly heavier across seasons and regions in the control plots (0.6^{d} g per pod) compared with plots mulched with *Senna* (0.5^{d}) and *Imperata* (0.5^{d}) ($F = 9.2^{**}$).

Pod yield. Dry matter pod yield among regions was not distinct across seasons but rather interacted with them. For season I/95, I/96, and I/97, Tokpa/Ayou yielded significantly highest total pod weight compared with IITA and Lema; the latter was also significantly lower in yield than IITA ($F = 23.6^{**}$) (Table 6.3a.). This differed for the late seasons, where IITA

showed significantly best results in season II/95, superior to Tokpa/Ayou and Lema. Lema again scored significantly lowest. Lema revealed best results after the harvest of season II/96, which was significantly more than at IITA and in Tokpa/Ayou.

Grain yield. The patterns were almost the same as for pod yields with weaker expression of certain differences ($F = 24.6^{**}$). Tokpa yielded significantly highest during seasons I/95 and I/96 with $1{,}046.0^{d}$ kg per hectare and $1{,}014.8^{d}$, respectively (Table 6.3b.). In contrast, Lema scored significantly lowest for seasons I/95, I/96, and I/97. No significant variation occurred during season II/95 since values were about zero. Lema yielded highest in season II/96 and was significantly distinct from results in Tokpa/Ayou.

On-farm regions

Total pod numbers. NPK exhibited a significantly different influence between the two on-farm regions, Tokpa/Ayou and Lema, when compared across seasons ($F = 5.2^{**}$) (Table 6.4.). Season II/95 did not show any significant variation between regions or NPK levels. NPK significantly increased pod numbers in season I/96 in both regions, but plots with NPK in Lema did not significantly deviate from non-fertilized plots in Tokpa/Ayou. Season II/96 showed a sandwich-like pattern indicating that fertilized plots in Lema counted significantly more pods than non-fertilized ones in the same region and they were also significantly superior to both NPK levels in Tokpa/Ayou. In turn, non-fertilized plots in Lema remained significantly below both NPK levels in Tokpa/Ayou. Within Tokpa/Ayou, no significant variation occurred between NPK levels although a slight increase due to fertilizer was visible. Fertilizer application within Lema led to significantly reduced pod numbers in season I/97. A slight increase was observed for Tokpa/Ayou, but this was not significant.

Pod weight. NPK showed impact among seasons. The significant interaction indicated an inverse reaction between season II/96 and season II/95, I/96, and I/97 due to fertilizer application ($F = 3.8^{*}$) (Table 6.5.). Whereas in season II/96 NPK resulted in an increase of pod weight from 0.53^{d} g per pod to 0.67^{d} when fertilizer was applied, pods were slightly lighter in the remaining seasons due to NPK. The decrease in weight was not significant for season II/95 but was significant in season II/96.

Pod yield. An assessment of the influence of NPK showed that significant interaction occurred with season ($F = 4.1^{**}$) (Table 6.6.). No significant variation was observed in seasons I/95, II/95, and I/97. The application of fertilizer resulted in significantly higher pod yields in seasons I/96 and II/96.

Grain yield. A marginal interaction occurred between the two regions among seasons when assessing NPK fertilizer levels ($P \geq 0.05$). NPK did not show effect on yields in seasons I/95, II/95, and I/97. Interaction occurred between the two regions for seasons I/96 and II/96 on NPK levels. In season I/96, Tokpa/Ayou yielded more in fertilized plots but no effects were

observed in Lema. This was opposite in season II/96, where Tokpa/Ayou did not reveal differences but fertilizer increased yields in Lema.

Seasonal differences within the same region

Tokpa/Ayou

Total pod numbers. Counting of pod numbers was started in season II/95. All seasons varied significantly among each other ($F = 61.1^{**}$) (Table 6.7.). Season I/96 recorded highest pod numbers and II/95 lowest. Early growing seasons (I/96, I/97) counted significantly more pods than late seasons (II/95, II/96). A three-way interaction occurred including season, NPK, and mulch ($F = 2.5^{*}$). No attempt was made to fully formulate all the differences since the comparison and the main factors were of primary interest. This interaction demonstrated that there were no principal NPK or mulch effects across seasons. To better explain these interactions analysis was carried out on a per-season basis; the results are presented later in this chapter.

Pod weight. Pod weights varied significantly among seasons ($F = 60.7^{**}$). Seasons I/96, II/96, and I/97 were significantly different from each other (Table 6.2.). Mulch had an impact on weight across seasons, indicating that pods in the control generally were significantly heavier (0.91^{d}) than in *Senna* mulch (0.76^{d}) ($F = 5.5^{**}$). Season II/95 was discarded from analysis since only one event with low pod weight occurred.

Pod yield. A distinct variation among seasons was observed. First growing seasons highly exceeded late seasons ($F = 217.1^{**}$). Within first seasons, I/95 and I/96 did not suggest significant deviation from each other but both yielded significantly better than season I/97. Within late seasons, which both yielded very low, no significant difference was found. An alleged NPK effect was dissolved upon investigation of its interaction with mulch across seasons (Table 6.8a.). When combined with fertilizer, the control and *Imperata* were always significantly higher than all treatments without NPK ($F = 4.3^{*}$). Within non-fertilized plots, differences were not significantly distinct but investigation of fertilized plots separately marked the control and *Imperata* as both yielding significantly more than *Senna*. Season II/95 was discarded from analysis as mentioned above.

Grain yield. Seasonal differences followed the patterns for pod yields. Early growing seasons were significantly better in yields than later seasons ($F = 244.1^{**}$) (Table 6.3b.). Among early seasons, I/97 resulted in significantly lower weights than seasons I/95 and I/96, which were close together. A suspected NPK effect turned out to interact differently with mulch (Table 6.8b.). *Imperata* in combination with fertilizer always yielded significantly more than all non-fertilized treatments and the fertilized control also scored higher than mulch of *Senna* and *Imperata* without fertilizer ($F = 3.2^{*}$). Within non-fertilized plots, differences were

not significantly different whereas among fertilized mulch treatments, *Senna* recorded significantly lower yields than the control and *Imperata*; neither differed significantly.

Lema

Total pod numbers. In contrast to Tokpa/Ayou, the clustering for early and late growing seasons did not appear in Lema. Season I/96 yielded significantly highest compared with all other seasons, followed by II/96, which was significantly superior to I/95, II/95 and I/97. Season I/97 scored significantly better than seasons I/95 and II/95, and the latter two did not deviate significantly from each other ($F = 28.2^{**}$). Across all five seasons, mulch treatments interacted with NPK (Table 6.9.). The fertilized control was significantly superior to all other treatments ($F = 4.5^{*}$). Within non-fertilized plots, significance did not occur and among fertilized ones both mulch treatments *Senna* and *Imperata* were similar.

Pod weight. Season II/96 resulted in significantly heaviest pods compared with all other seasons followed by I/96, which scored significantly higher than seasons II/95 and I/97 ($F = 23.7^{**}$) (Table 6.2.). The latter two did not show significant variation. NPK levels interacted with season, indicating that pod weights in season I/96 decreased through fertilizer application whereas they increased in season II/96 when fertilizer was used ($F = 3.4^{*}$). All the other seasons resulted in non-significant variation between NPK levels.

Pod yield. Seasons I/96 and II/96 recorded highest pod yield and were similar to each other. They yielded significantly better than seasons I/95, II/95, and I/97 ($F = 12.6^{**}$). The latter three seasons did not differ significantly among each other. NPK levels were significantly different in season II/96 only where fertilized plots reacted with an increase in yield ($F = 3.3^{*}$).

Grain yield. A comparison of seasons indicated that seasons I/96 and II/96, which were similar, resulted in significantly more grain yield than seasons I/95, II/95, and I/97 ($F = 11.4^{**}$) (Table 6.10.). The latter three seasons did not suggest significant variation among each other. A three-way interaction on seasons, NPK levels, and mulch treatments indicated that in season I/95 no significant variation occurred within non-fertilized plots. For fertilized plots, the control was significantly superior to *Senna* while *Imperata* remained in between. When the control was combined with fertilizer, it scored significantly higher than either the control or *Imperata* without NPK. Season II/95 did not reveal any measurable grain yield. An assessment of season I/96 showed that the only significant difference occurred within non-fertilized plots, where the control recorded better weights than *Senna*. Investigations for season II/96 displayed no significant variation within non-fertilized plots. When fertilizer was used, yields from *Imperata* treatments were significantly lower than those of the control and *Senna*, both without significant difference. Across both NPK levels, the control with fertilizer was significantly superior to all treatments without NPK. Fertilized plots with *Senna* mulch yielded significantly better than the unfertilized control and *Imperata*. This complex interaction was significant ($F = 2.2^{*}$). A significant difference occurred in season II/96 between fertilizer levels across mulch, where

yields could be improved through use of NPK ($F = 3.4^{*}$). Variation was not significant in season I/97.

IITA

Total pod numbers. Counting pod numbers was started in season II/95. Early seasons yielded significantly more pods than late seasons, but the variation within each cluster was not significant ($F = 29.9^{**}$).

Pod weight. Comparison by seasons showed that II/95 recorded significantly lighter pods (0.3^{d} g per pod) than s I/96 (0.7^{d}), II/96 (0.8^{d}), and I/97 (0.9^{d}), the latter three not greatly differing among each other ($F = 6.4^{*}$). Mulch varied in favor of the control (0.75^{d}), which had significantly heavier pods than mulch treatments *Senna* (0.60^{d}) and neem (0.65^{d}) ($F = 4.7^{*}$).

Pod yield. A strong variation among seasons resulted in significantly more pod yield for early seasons than late ones ($F = 19.3^{**}$). Within early seasons, I/95 reached significantly highest levels compared with seasons I/96 and I/97; the latter two were similar. No significant deviation was found within late seasons.

Grain yield. Exactly as was found for pods, grain yields varied considerably among seasons ($F = 14.2^{**}$) (Table 6.11.). Early seasons resulted in significantly higher yield than both late seasons. Season I/95 doubled seasons I/96 and I/97 and was significantly superior to all other seasons. Within early seasons, I/96 and I/97 revealed about the same weight and the same was true for both late seasons at a far lower level.

Differences within seasons

Tokpa/Ayou

First season (I/95)

Total pod numbers. Plants under *Imperata* mulch produced significantly more pods than those of the control ($F = 6.5^{*}$). *Imperata* was marginally superior in pod numbers to *Senna*.

Grain yield. The same pattern among mulch treatments that was observed for pod numbers applied for grain yields. *Imperata* yielded significantly better than the control and *Senna* remained marginally below *Imperata* ($F = 5.9^{*}$).

Second season (II/95)

Total pod numbers. No significant differences were found due to treatments. Pod numbers were comparatively low in this season.

Grain yield. Except for one observation with 2 g fresh weight on 127 pods, no weight could be obtained at all. Since pods were small and underdeveloped, the few grains that could be isolated did not result in any weight to a precision of 0.0 g.

Third season (I/96)

Total pod numbers. Pod numbers were increased through fertilizer application by about 25% ($F = 31.4^{**}$).

Pod weight. Weights per pod varied differently among mulch treatments due to NPK levels (Table 6.13.). Within non-fertilized plots, the control recorded significantly lighter pods than both mulch treatments, which were similar. Within plots with NPK application, variation was not strong. Pods in the control without fertilizer weighed significantly less than all the other treatments. This interaction was significant ($F = 6.0^{*}$).

Pod yield. Yields of pods were increased significantly – about 30% – in plots where fertilizer was applied ($F = 39.2^{**}$).

Grain yield. NPK application significantly increased grain yields by about 30% as was observed for pod yields ($F = 35.8^{**}$). Without fertilizer, 884.9 kg per hectare were yielded, which was improved to 1,157.4 due to NPK.

Fourth season (II/96)

Total pod numbers. Treatments did not suggest any effect on numbers of pods per 50 plants.

Pod weight. Pod weights were comparatively low, with 0.25 g per pod in the mean, and did not show significant variation among treatments.

Pod yield. Pod yields did not reveal significant variation among treatments.

Grain yield. As was the case for pods, variation of grain yields was not significant (Table 6.14.). No treatment impact was suggested. In general, yields were very low in this season. However, a slight interaction was visible for *Senna* versus the control and *Imperata* when comparing NPK levels. *Senna* dropped in yield due to fertilizer, in contrast with both other treatments.

Fifth season (I/97)

Total pod numbers. Pod numbers among mulch treatments varied differently between NPK levels, indicating a significant interaction with *Senna* versus the control and *Imperata* ($F = 12.8^{**}$) (Table 6.15.). Within non-fertilized plots, all treatments were significantly different

from each other, the control scoring highest and *Imperata* remaining lowest. When assessing fertilized plots, *Senna* remained significantly lower in numbers than the control and *Imperata*. Significantly more pods were counted on plants of the fertilized control than in both mulch treatments without NPK. Fertilizer application led to a significant improvement in pod numbers for *Imperata* mulch.

Pod weight. Pods were significantly heavier in the control (1.20 g per pod) than in both mulch treatments *Senna* (0.91) and *Imperata* (1.01) ($F = 7.1^{*}$). Within mulch, no significant variation was found.

Pod yield. Pod yields followed principally the findings for total pod numbers on the NPK*mulch interaction, which was significant ($F = 3.7^{**}$) (Table 6.16a.). Within non-fertilized plots, the control significantly exceeded both mulch treatments, which were not significantly different from each other. All treatments with fertilizer were significantly distinct from each other; the control obtained best results and *Senna* remained lowest. The fertilized control in general yielded significantly better than all mulch treatments with and without NPK. When comparing NPK levels, both mulch treatments, *Senna* and *Imperata*, recorded a significant but inverse difference. Whereas *Senna* significantly lost in fertilized plots, *Imperata* improved the pod yields at the same time.

Grain yield. The patterns for grain yield were more or less the same as for pod yields, but the interaction between NPK and mulch turned out to be not significant. There was rather a mulch main effect, which indicated that the control across NPK levels was significantly better in yields than both mulch types ($F = 7.1^{*}$) (Table 6.16b.). The visible tendencies, which showed a decrease in yield for the control and *Senna* when they received fertilizer, and the increase at the same time in *Imperata,* were not significant.

Lema

First season (I/95)

Total pod numbers. Pod numbers remained very low during this season and did not show significant treatment impact.

Pod yield. Treatments were not significantly distinct from each other.

Grain yield. As observed for pod yields, results for grains did not suggest significant variation due to treatments. Yields were generally very low, with an extrapolated weight over-all of 13.0^{d} kg per hectare.

Second season (II/95)

Total pod numbers. The results for this season were worse than those for the preceding season (I/95). Very low pod numbers of about 11 pods per 50 plants were harvested, mainly due to results from one replication.

Pod weight. Most of the pod numbers per 50 plants did not reveal any weight in gram to one digit after the decimal point. Analysis therefore did not suggest any significant variation among treatments. The overall pod weight was 0.05 g per pod.

Pod yield. No significant variation was found on the generally very low results.

Grain yield. Except for two observations, grain weight on 50 plants could not be estimated to the precision of 0.0 g.

Third season (I/96)

Total pod numbers. Due to NPK application, pod numbers increased by about 70% ($F = 18.6^{**}$).

Pod weight. Mulch treatments responded differently due to NPK levels, indicating that the non-fertilized control had significantly highest pod weights compared with all other treatments ($F = 5.6^{*}$) (Table 6.17.). Within non-fertilized plots, the control resulted in marginally heavier pods than *Senna* but was clearly higher in weight than *Imperata*. Both mulch types did not vary significantly. Fertilized plots were close in weights. Only the control displayed a significant impact due to NPK levels, as pod weight dropped significantly when fertilizer was applied.

Pod yield. Pod yields were not significantly distinct among treatments.

Grain yield. In the same way as for pods, the variation in grain yields was not significant. The yields were comparatively low, with an equivalent of 210.3 kg per hectare on average.

Fourth season (II/96)

Total pod numbers. Pod numbers increased through fertilizer application by about 100% ($F = 11.3^{**}$).

Pod weight. Lowest pod weights were recorded in *Imperata* mulch with 0.71 g per pod and were significantly less than for the control (1.22) and *Senna* (1.25), which remained close together ($F = 6.4^{*}$).

Pod yield. Total pod yield per 50 plants increased more than 2.5 times in plots with fertilizer ($F = 11.5^{**}$).

Grain yield. In plots where NPK was applied, yields increased almost threefold from an equivalent of 71.6 kg per hectare to 208.5 in fertilized plots ($F = 10.5^{**}$). However, even in fertilized plots the level was very low.

Fifth season (I/97)

Total pod numbers. Due to NPK application, pod numbers dropped by about 50% ($F = 5.1^{*}$). Significantly more pods were produced in the control than in *Senna* and *Imperata*: 2.3 times the number for *Senna* and four times that of *Imperata* ($F = 8.3^{**}$). Both mulch types did not differ significantly.

Pod weight. In addition to the higher pod numbers, pods were also significantly heavier in the control (0.25 g per pod) than in *Imperata* (0.12) and *Senna* (0.11) (18.7^{d}) ($F = 6.8^{*}$).

Pod yield. Fertilizer application proved to be disadvantageous to pod yields, resulting in a decrease of more than 50% in fertilized plots ($F = 6.4^{*}$). The control revealed significantly the best output compared with mulch treatments *Senna* and *Imperata*, which did not differ significantly from each other ($F = 14.5^{**}$).

Grain yield. Similar to findings on pod yields, fertilizer impact reduced grain yields by almost 90% across mulch treatments ($F = 8.4^{*}$) (Table 6.18.). The control yielded significantly highest compared with mulch types, which did not differ significantly from each other ($F = 18.6^{**}$).

IITA

First season (I/95)

Total pod numbers. No significant differences occurred among mulch treatments.

Pod yield. Treatments did not influence pod yields significantly.

Grain yield. The same applied for grain yields. The recorded differences among the control (664.8 kg per hectare), *Senna* (746.3), *Imperata* (881.8), and neem (666.5) were not significant.

Second season (II/95)

Total pod numbers. Pod counts resulted in comparatively low numbers, the variation of which could not be separated by treatments.

Pod weight. The control (0.38 g per pod) and *Imperata* mulch (0.38) developed significantly heavier pods than *Senna* (0.20) and neem (0.26) ($F = 15.0^{**}$). Within both pairs, variation was not significant.

Pod yield. Generally, low pod yields did not suggest any significant impact by treatments.

Grain yield. The same patterns that were isolated for pod weights applied for grain yield as well. The control (10.4^{d} kg per hectare) and *Imperata* (17.0^{d}) were significantly better in yield than *Senna* (0.9^{d}) and neem (1.9^{d}) ($F = 7.1^{*}$).

Third season (I/96)

Total pod numbers. Significant variation among treatments did not occur.

Pod weight. All treatments yielded similar pod weights with 0.7[d] g per pod.

Pod yield. Treatment differences were not observed for yields on pods.

Grain yield. Grain yields remained low with 416.2 kg per hectare in the control, which was slightly more than for *Imperata* (366.3), neem (341.3), and *Senna* (271.1). However, this small variation among treatments together with a high variation was not of significant importance.

Fourth season (II/96)

Total pod numbers. Mulch treatments did not show significant impact on pod numbers.

Pod weight. Slight variation in pod weights between the control (0.9 g per pod), *Senna* (0.8), *Imperata* (0.7), and neem (0.7) was not significant.

Pod yield. Pod yield was not significantly different among treatments.

Grain yield. Yields of grain dry matter remained at low levels without distinct variation among the control (97.7 kg per hectare), *Senna* (96.1), neem (59.6), and *Imperata* (20.0).

Fifth season (I/97)

Total pod numbers. Significant deviation was not observed among treatments.

Pod weight. Pod weights were close together for *Imperata* (0.95 g per pod), the control (0.92), neem (0.92), and *Senna* (0.87).

Pod yield. Variation due to treatments was not significant.

Grain yield. As was the case for pods, grain yields remained low and close together among treatments. Plants with mulch recorded slightly more weight in *Imperata* (389.0 kg per hectare), *Senna* (372.8), and neem (365.0) compared with the control (258.1). However, this was not significant.

Discussion

Regional differences

Total pod numbers. Tokpa/Ayou, which yielded highest pod numbers compared with both other regions, revealed highest flower counts (Chapter 2) and lowest thrips densities (larvae + adults) per flower. Flower shedding, which is a main consequence of thrips attack (Taylor 1964; Wien & Tayo 1979; Tamò et al. 1993b; van de Klashorst & Tamò 1995), can be assumed lower than in Lema and at IITA. Early seasons in Tokpa/Ayou, IITA, and Lema (ex-

cepting season II/96) resulted in higher pod numbers, which followed the increased thrips abundance during the year (Chapter 3) (Summerfield et al. 1974; Tamò et al. 1993b) and thus attacks on flowers became more severe in late seasons through subsequent flower shedding (Wien & Tayo 1979; van de Klashorst & Tamò 1995). Lema represented an exception with pod numbers in season II/96 that were higher than in I/97. This was attributable to fewer thrips larvae in season II/96 given a similar number of flowers.

Pod weight. IITA resulted in heaviest pods during season II/95 only because Lema and Tokpa/Ayou yielded very low with small pods accounting for almost no weight. Lightest pods were measured in Tokpa/Ayou for season II/96 together with higher pod numbers compared with Lema and IITA. As seed weight is negatively correlated with number of pods per plant (Rachie & Roberts 1974), higher pod numbers in Tokpa/Ayou might have accounted for this. Lema remained at lowest pod weights in season I/97. Thrips abundance was highest in this region and remained at moderate to higher levels during three weeks, whereas it sharply peaked in Tokpa/Ayou and at IITA. A constant loss of flowers, which could not develop into pods, and the compensatory growth (Wien & Tayo 1979) probably increased the proportion of young pods with low weight. The control recorded overall higher weights per pod as pod numbers across regions and seasons were lower than in mulch treatments.

Pod and grain yield. Yields of pods and grains were almost identical and were much higher in Tokpa/Ayou in all early growing seasons than in Lema and at IITA. Pod numbers were always higher in these three seasons for Tokpa/Ayou (as flowers were more abundant, too) and pod weight was higher in seasons I/96 and I/97. Pods per plant, seeds per pod, and seed weight account for 83% of variation in yield as stated by Janoria & Ali (1970), whereas the number of pods per plant in particular was suggested as the most important explanatory variation in total seed yield by Littleton et al. (1979b) and Summerfield et al. (1978). Thus, the corresponding pod numbers for the different regions can basically account for these differences in yield. As for season II/96, Lema revealed about the same pod numbers but the weight per pod was much higher, therefore accounting for comparatively higher pod and grain yields.

On-farm regions

Total pod numbers. More pods in season I/96 in fertilized treatments across regions were the result of overall more flowers (Chapter 2), although more thrips larvae were counted in these plots, too. A higher plant vigor might have led to a higher carrying capacity of thrips in flowers. Subsequently, the plants still produced more flowers (Summerfield et al. 1983; Summerfield & Roberts 1983). Season II/96 revealed a clear increase of pod numbers in Lema through fertilizer application. This was attributable to more flowers and bigger plants in these NPK plots, which accounted for an increased phenological potential (Chapter 2) (Summerfield et al. 1983; Summerfield & Roberts 1983). Soils were much poorer in cation exchange capacity (CEC) and in carbon, nitrogen, and magnesium quantities (Table 2.1.) and were expected to

respond significantly to chemically applied nutrients (Chapter 2). In fact, Lema was the only region where soils were judged very poor in nitrogen using the standards of Ministère de la Coopération et du Développement, République Française (1991). Plant vigor was probably improved by fertilizer application. In turn, soils in Tokpa/Ayou were much better supplied with basic nutrients and did not respond significantly in pod numbers since there was neither an increase in flower numbers nor remarkable changed in plant size through NPK. Fertilized treatments in Lema in season II/96 carried more pods than Tokpa/Ayou in general, attributable to the fact that highest flower numbers were produced on comparatively biggest plants in Lema in NPK plots. With the fertilizer treatment, pod numbers on plants were reduced in Lema in season I/97. On the basis of similar flower numbers but higher counts for thrips larvae (Chapter 3), the flower shedding was expected to be higher and less pod set was assumed. More flowers may have been dropped due to thrips attacks in NPK plots although they were counted initially.

Pod weight. Despite the negative relationship between pod weight and pod number (Rachie & Roberts 1974), fertilizer application in season II/96 led to increased pod weight together with higher pod numbers across seasons and both regions. This suggests a positive fertilizer effect on flower numbers and pod filling. The effect of NPK was contrary in season I/96 and I/97, where pod weights dropped slightly in fertilized plots. Higher larval numbers in fertilized treatments probably caused more flower shedding and resulted in higher compensation, which might have increased the proportion of small pods.

Pod and grain yield. Pod yields increased through use of fertilizer in seasons I/96 and II/96, although larval abundance of thrips was higher except for season I/96 in Tokpa/Ayou. Flower numbers were also higher in both seasons for both regions except for Tokpa/Ayou in season I/96, where no change occurred. The fact that fertilized treatments showed higher pod numbers as a result might be attributable either to a higher carrying capacity of flowers for thrips (Tamò et al. 1993b) or a better compensation by plants for losses due to higher vigor through applied nutrients (Wien & Tayo 1979). In addition to the general correspondence between pod and grain yield, grain yields were not different in season I/96 for Lema, probably because of lower weights of pods in fertilized treatments. It is likely that lower pod weights negatively compensated for higher pod numbers. Grain yields in Tokpa/Ayou did not follow the differences in pod yields in season II/96. Fertilized plots yielded hardly more pods than non-fertilized ones and pods were only slightly heavier in NPK plots. These pods were very small for both NPK levels. It is suggested that the husk of the pod was principally contributing to differences in yields in this particular case, as the husked grains showed about the same results.

Seasonal differences within the same region

Tokpa/Ayou

Total pod numbers. Early cropping seasons revealed more pods than late seasons, which was the consequence of lowest thrips abundance and highest flower production in early seasons. As the thrips population increases throughout the year (Tamò et al. 1993b), the pest pressure on cowpea increases in parallel (Summerfield et al. 1974), leading to higher flower shedding in late seasons (Taylor 1964; van de Klashorst & Tamò 1995). Reduced pod set was the result of higher thrips attacks. Among seasons, I/96 recorded highest pod set while counts of thrips larvae remained lowest. Flower shedding was reduced therefore. In contrast, season II/95 yielded lowest pod numbers since larval abundance reached the highest levels among seasons (Chapter 3) but flower numbers remained at second-lowest levels (Chapter 2) due to increased shedding after thrips attacks (Tamò et al. 1993b). A soilborne influence was excluded completely.

Pod weight. Weights per pod were highest in season I/96 followed by I/97 and II/96. Thrips abundance increased in the same order. As a result, flower numbers were highest in season I/96 but lowest in II/96. This followed from the respective thrips damage, as pod set was reduced due to thrips pressure. As the plant compensated for losses in reproductive tissue (Wien & Tayo 1979), the proportion of younger pods, which appeared after early flowers were lost, was presumably higher at harvest. Hence, pod weight was lower the higher the pest abundance had been, the losses of which the plant compensated for. The control recorded heaviest pods across seasons although slightly fewer flowers were counted throughout the season. The lower thrips pressure in the control probably caused less severe damage to flowers so that the proportion of lost flowers through shedding decreased. Due to the negative correlation of pod weight to pod number (Rachie & Roberts 1974), the comparatively lower flower numbers in the control could have resulted in heavier pods.

Pod and grain yield. Straightforward from the results in pod numbers and pod weight, which indicated more and heavier pods for early seasons, followed the corresponding pod and grain yields. Pod numbers per plant and seed weight are among the major factors accounting for most of the variation in cowpea yields (Janoria & Ali 1970). In the assessment of fertilized plots separately, *Senna* resulted in lowest yields across seasons while accounting for lowest pod numbers and pod weights, with both factors strongly influencing yield. Although *Senna* had higher flower numbers than *Imperata*, comparatively highest thrips abundance was responsible for poorest pod set.

Lema

Total pod numbers. Seasons I/96, II/96, and I/97 revealed highest pod numbers in decreasing order compared with I/95 and II/95 as flower counts remained at lowest levels in both last-mentioned seasons. The decreasing order in flower numbers for the remaining seasons was I/96, I/97, and II/96 – a different order from pod numbers. Despite lower flower numbers than I/97, season II/96 recorded lower abundance of thrips larvae than I/97. The flower shedding was thus expected to be lower and accounted for a better pod set in season II/96. For fertilized treatments separately, the control yielded slightly more pods than both mulch treatments, which was also the result of more flowers in the control. Slightly more thrips larvae in the control were assumed as a result of a higher carrying capacity of plants in these plots. Since larval densities per flower remained lower in the control, the damage and subsequent flower shedding were likely to result in better pod set.

Pod weight. Despite more pods in seasons I/96 and II/96, the weight per pod was also higher than in other seasons. Because the abundance of thrips larvae remained lower in these two seasons. Hence, plants were assumed to compensate less for damages while setting pods from early flowers, which matured better until the time for harvest. Pod weights increased thereby to higher levels. In general, the younger flowers that appear in the second half of anthesis contribute very little to final grain yield (Ojehomon 1968; Summerfield & Roberts 1983). This refers to pod numbers and weight per pod. Late flowers are less likely to produce pods since principally the first two flowers per inflorescence set fruits. They receive more assimilates to the detriment of younger ones (Summerfield & Roberts 1983; Summerfield et al. 1983). If thrips attacks start early, these early flowers are lost. Although cowpea theoretically can produce flowers indefinitely until the plant dies (Ojehomon 1968), the pods produced by later flowers are smaller and still not ripe at the time of harvest. The method of harvesting, which followed common standards to interfere when more than two-third of the pods were ripe (Duke 1990), strongly biased the pod weights. Overall low pod weights at the time of harvest were therefore likely to be accounted for by early and high pest abundance. Lighter pods in fertilized plots in season I/96 compared with non-fertilized treatments but heavier pods in fertilized plots in season II/96 were linked to thrips densities per flower. No density differences of thrips occurred in flowers in season I/96 among NPK levels. Fertilized plots had more flowers and higher thrips abundance in this season. Larval densities in season II/96 were lower in non-fertilized plots on lower flower numbers. The latter accounted for more damage through higher larval pressure and thus smaller pods, which probably resulted from more compensation of the plant in non-fertilized plots. In season I/96, more larvae in fertilized plots could have led to more flower shedding in these plots. As compensation increases through damage, the proportion of smaller pods is expected to be higher.

Pod and grain yield. Pod and grain yield was basically influenced by pod numbers and showed the same patterns for seasons. Seasons I/96 and II/96 yielded more pods and grains

than seasons I/95, II/95, and I/97. Number of pods is among the factors that principally explain cowpea yields (Janoria & Ali 1970; Littleton et al. 1979b). The low yields in season II/95 and season I/97 may be explained additionally by the time at which thrips larvae reached their peak. The larval peak in both seasons occurred at DAP 49 and was about one week earlier than in seasons I/96 and II/96. As noted above, early damage to flower buds or flowers is likely to have greater impact on final pod yield because generally only the first two flowers produce fruits (Summerfield & Roberts 1983). Within fertilized plots, the control yielded more grains since more flowers were produced throughout the season (Chapter 2) and finally more pods were set; the control thus recorded more weight than both mulch treatments. Fertilized treatments in season I/96 indicated more yields for the control than for *Senna*. Whereas flower and eventually pod numbers were lower, pod weight reached double the level in the control as in *Senna*. When multiplying pod numbers by pod weight, this resulted in higher yield for the control. Lower grain yield in season II/96 for *Imperata* within fertilized plots may be explained principally by flower numbers and subsequent pod set, and pod number as well as pod weight, which was lower in *Imperata* as for the control and *Senna*. As larval thrips density per flower was higher in *Imperata*, too, this probably caused increased flower shedding, which led to lower flower numbers in *Imperata*. For pod and grain yield respectively, season II/96 displayed a NPK effect in favor of fertilized treatments. More and heavier pods followed higher flower counts throughout the season (Chapter 2). Fertilized plots revealed lower larval thrips density per flower, which certainly allowed the higher flower numbers in these plots.

IITA

Total pod numbers. Higher pod numbers were obtained in early seasons than in late seasons against the background of thrips abundance and subsequent flower damage, which was generally higher in late seasons (Chapter 3). This was due to increased flower shedding in late seasons (Chapter 2).

Pod weight. Pod weight in season II/95 was lower than in seasons I/96, II/96, and I/97 as thrips abundance in season II/95 was also much higher than in the remaining seasons. High pest pressure probably led to permanent flower shedding while causing considerable compensation efforts by the plants. It was assumed that the proportion of young pods originating from later flowers due to compensation was relatively higher and decreased the pod weights in the mean. Later flowers receive fewer assimilates (Summerfield & Roberts 1983) and lag behind in development. Slightly heavier pods were obtained from plants in the control than in *Senna* and neem across seasons. Lower larval abundance was recorded for the control in parallel thus accounting for less flower damage and probably reduced compensation by the plants. This probably increased the proportion of normally maturing pods. However, differences in pod weights were not important from a biological point of view, although they were statistically significant.

Pod and grain yield. Principally following the patterns for pod numbers, pod and grain yields in early seasons exceeded those in late seasons due to correspondingly higher thrips attacks in late seasons, the latter suffering more flower shedding as thrips populations accumulate throughout the year (Summerfield et al. 1974; Tamò et al. 1993b). Among the early cropping seasons, highest yields were obtained in season I/95, which could be explained by the comparatively lower larval thrips densities per flower and thus less flower damage.

Differences within seasons

Tokpa/Ayou

First season (I/95)

Total pod numbers. Highest pod numbers were obtained for *Imperata* as lowest thrips abundance likely reduced flower damage and subsequent shedding of flowers in this treatment, in spite of only small differences in flower numbers among treatments.

Grain yield. Principally following pod numbers, grain yields were higher for *Imperata*. Number of pods is one of three main factors that basically explain variation in total grain yield (Janoria & Ali 1970; Littleton et al. 1979b). Although not significantly different from season I/96, this season revealed maximum yields among all seasons in this region. Together with second highest pod counts from phenological studies (Chapter 2), better nutritional conditions were responsible for these high yields. Highest values for cation exchange capacity (CEC) and phosphorus as well as slightly less acid soils certainly augmented the vigor of the plants. Since thrips abundance was comparatively high, the carrying capacity for pests was increased (Tamò et al. 1993b) still resulting in better yields.

Second season (II/95)

Total pod number and grain yield. Although pods appeared on the plants, their numbers were low and they were entirely underdeveloped. Grains did not record any weight after husking and the yield can be considered zero.

Third season (I/96)

Total pod numbers. The increase of pod numbers due to NPK fertilizer was possible as a result of lower larval thrips densities per flower on the one hand and the improved soil conditions after chemically applied nutrients on the other hand.

Pod weight. Although differences in weight between mulch and the control were statistically significant, their biological variation was not important and could have stemmed from variation in soil conditions.

Pod and grain yield. The effect of fertilizer on pod numbers basically led to increases in pod and grain yields in the same way. Pods were also slightly heavier in fertilized treatments and accounted additionally for better results. Both factors principally influence cowpea yields (Janoria & Ali 1970).

Fourth season (II/96)

Total pod numbers. Similar to results in season II/95, pod numbers remained very low in this season. Higher thrips pressure throughout the year was responsible (Summerfield et al. 1974; Tamò et al. 1993b) as it severely increased flower shedding.

Pod weight. The overall low pod weight indicated a high proportion of underdeveloped pods as the plants compensated for permanent losses in flowers. Many of these pods were dry but very small and suggest that the reduced amount of assimilates for later flowers (Summerfield & Roberts 1983; Summerfield et al. 1983) did not allow full maturity of these delayed pods.

Fifth season (I/97)

Total pod numbers. Within non-fertilized plots, the control yielded the highest pod numbers and *Imperata* the lowest. A clear relationship to thrips abundance was not found. The control had the lowest flower numbers and also the lowest abundance of thrips larvae, but the highest larval density per flower. This season also recorded the lowest phosphate levels in the soil, which might have been the reason fewer flowers were supported by the plants. Flower counts in *Imperata* revealed comparatively the highest numbers. Ojehomon (1968) reported that the proportion of flowers that are shed before they can set pods increases with total flower numbers per plant. A better pod set per flowers produced is likely to have occurred in the control because of the overall lowest flower numbers. Within fertilized plots, *Senna* yielded the lowest pod numbers. Larval abundance exceeded levels for other treatments and the flower numbers were higher, too. High thrips damage together with naturally more flower shedding (Ojehomon 1968) was probably the most likely reason for poor pod set in this treatment.

Pod weight. Slightly heavier pods were obtained from plants of the control although more pods were harvested from these plots, too. This suggests, based on the negative relation between pod number and pod weight (Janoria & Ali 1970), that the yield potential still was not met. None of these factors was probably limiting for the other. On the one hand, thrips abundance (larvae and adults) was lower in the control and possibly caused less compensatory growth by the plant, which would have resulted in a higher proportion of underdeveloped pods. On the other hand, values for phosphate were slightly higher in the control compared

with both mulch treatments. The element phosphorus is important for the generative phase of plant growth (Vogel & Angermann 1967; Finck 1969) and thus probably supported better developed pods. Phosphorus also improves nodulation and hence nitrogen fixation (Wien & Summerfield 1984; Cadisch et al. 1989).

Pod and grain yield. Pod and grain yields were higher in the control compared with both mulch treatments as the number of pods and weight per pod were higher in the control, too. Both measures contribute to cowpea yield (Janoria & Ali 1970; Littleton et al. 1979b). Pod yields within fertilized plots were significantly different between both mulch treatments. This was ascribed to a NPK effect, which resulted in a different husk weight in favor of the control and *Senna*. When the grains were husked, these differences among both mulch treatments disappeared.

Lema

First season (I/95) and second season (II/95)

Total pod number, pod weight, and pod and grain yield. Pod numbers remained very low in both seasons. Measurements taken in and around the fields did not furnish explanations for low pod numbers and yields in season I/95. Season II/95 recorded its larval maximum at DAP 49 (Chapter 4), which was the time of early flowering (Chapter 3), thus being a delicate moment for pest attacks with remarkable consequences on final yield. A considerable diversity of wild host plants around the cowpea plots (Fig. 7.8.) (Chapter 7) was assumed to enhance a population build-up. Pod weights as well as pod and grain yield remained close to zero. Both seasons recorded lowest flower numbers among seasons and lowest abundance of thrips larvae. As for season II/95, it can be suggested that very early thrips attacks in flower buds (Chapter 3) suppressed flower development through increased shedding. Since flower numbers remained very low due to permanent damage, an important thrips population could not be supported throughout the season on cowpea. In fact, several important alternative host plant species with very high population levels accompanied growing cowpea in the vicinity (Fig. 7.8.) (Chapter 7). High levels of adult thrips were observed at DAP 49 in cowpea, but these dropped over the following weeks (Fig. 3.7.) (Chapter 3). This seems to confirm early and high migration activity of thrips, which might have caused severe damage. As flower numbers in cowpea also dropped after DAP 49, feeding and breeding conditions in cowpea became unfavorable and caused thrips to migrate back into wild hosts.

Third season (I/96)

Total pod numbers. Fertilizer application increased pod numbers as more flowers were counted in fertilized treatments. In addition, beneficial effects of applied nutrients may have

supported the sustenance of relatively more flowers in these plots. Under natural conditions, 70-88% of all flowers produced are shed naturally (Ojehomon 1972; Rachie & Roberts 1974). Additional nutrient supply is likely to increase the number of flowers that can be maintained by the cowpea plant; phosphorus in particular enhances nodulation (Giller et al. 1998).

Pod weight. The control in non-fertilized treatments revealed highest pod weights across all other treatments and recorded overall lowest flower and pod counts. It is likely that, due to the limited soil fertility in Lema, the negative correlation between pod numbers and pod weight (Littleton et al. 1979b) favored the control. With the lower pod numbers, pods probably could develop better, which was the opposite of all other treatments. Although larval abundance of thrips was second lowest among all treatments, the density per flower reached highest levels. A higher carrying capacity of cowpea plants was assumed in the control.

Pod and grain yield. All treatments yielded similarly at a low level. However, this season recorded higher yields than all other seasons. This might be explained by a poor wild host plant environment around cowpea plots and a relatively late abundance peak of thrips larvae, which occurred at DAP 56 (Fig. 3.8.) (Chapter 3). Early shedding of flowers was assumed to be reduced, resulting in better yields.

Fourth season (II/96)

Total pod numbers. More pods were obtained from fertilized plots, which was on the one hand the result of higher flower numbers and, on the other hand was believed to stem from a fertilizer impact on the ability of cowpea plants to sustain a higher flower number.

Pod weight. The fact that *Imperata* mulch recorded lowest pod weights was probably due to the combination of highest flower numbers and higher abundance of thrips larvae as well. Whereas higher flower numbers as a rule relate to lower pod weights (Janoria & Ali 1970; Littleton et al. 1979b), higher thrips attacks may lead to greater flower loss. As the plant compensates for losses in generative tissue (Wien & Tayo 1979), the proportion of smaller pods that do not mature by harvest is likely to rise.

Pod and grain yield. Straightforward from pod numbers and slightly heavier pods in fertilized plots, pod and grain yields were higher in NPK plots. As more flowers produced more pods and these pods also were heavier, both factors principally were responsible for these results (Littleton et al. 1979b). Since larval abundance of thrips was higher in fertilized plots, plants' tolerance for increased damage probably was enhanced through fertilizer, indicating a higher carrying capacity (Tamò et al. 1993b).

Fifth season (I/97)

Total pod number, pod weight, and pod and grain yields. Fertilizer application led to an overall decrease of all the factors that are principally responsible for cowpea yields. Plants in fertilized plots reached almost twice the size in NPK plots as in those without fertilizer. To-

gether with a considerable amount of rainfall during the season, plants developed much more vegetative tissue with fertilizer. Sellshop (1962) and Turk et al. (1980) emphasized that high soil fertility, particularly phosphorus, leads to high yields of vegetative mass but low fruit set. Therefore, plants without fertilizer reached higher flower and subsequently pod numbers, as well as greater pod weights and pod and grain yields. Since more thrips larvae and an increased larval density per flower were observed in fertilized plots, additional damage to the comparatively few flowers in these treatments was assumed. However, yields remained extremely low in general. This was explained by early rising thrips abundance (Fig. 3.10.) at DAP 42 (Chapter 3), which probably caused severe losses in flowers at an early stage. Considering the measures that determine cowpea yield, the control reached generally higher levels than both mulch treatments. Higher numbers in flowers resulted in best pod set and heaviest pods, which led to highest pod and grain yields consequently. However, when assessed separately, the underlying factors like flower numbers (Chapter 2) and thrips abundance (Chapter 3) did not vary significantly. They were rather believed to show a synergistic effect added throughout the season.

IITA

First season (I/95)

Neither total pod number nor pod and grain yield turned out to be significant. Mulch generally was judged to exert very weak influence on measures like pest abundance and flower production. Since fertilizer was not used in this region, the impact of mulch alone on these factors was expected to be of limited importance.

Second season (II/95)

Generally, low pod numbers due to thrips abundance, which rose throughout the season, did not show significant variation. Pods were slightly heavier in the control and *Imperata* than in *Senna* and neem. None of the principal factors like flower numbers, thrips abundance, or soil nutrients could explain these particular patterns. However, the difference was small and overall pod weights were very low. These patterns in pod weight determined final pod and grain yield, which showed differences accordingly. Grain yields were extremely low for all treatments.

Third season (I/96), Fourth season (II/96), Fifth season (I/97)

Throughout these three seasons none of the factors – total pod number, pod weight, and pod and grain yield – that are considered important for cowpea yield revealed any significant variation among treatments. Mulch in general proved to have no important impact on plant physiology (Chapter 2) or thrips abundance (Chapter 3). It was therefore not expected to lead

to important variation in pod and grain yield, which was basically a function of these two influences.

Conclusions

A basic complex was identified in this study that determined pod and grain yield of cowpea. The initial and most important component of this complex is the number of flowers produced by the cowpea plant. The total number of flowers was influenced by the production of vegetative mass, soil fertility, abundance of thrips, and the extent to which flowers are shed naturally. Sellshop (1962) and Turk et al. (1980) stated a negative relationship between soil fertility and seed yields. It was already concluded in Chapter 2 that NPK raises soil nutrients, especially nitrogen, which leads to vegetative overgrowth. This effect might be more emphasized on poor soils as was the case in Lema. Pest abundance, according to Booker (1965) and Ojehomon (1970), is the most important factor that causes yield losses in cowpea. In fact, the abundance of thrips and their respective density per flower were considered a crucial point for determining the number of flowers that are set and that finally produce pods. Increased pest abundance leads to severe damage and subsequent drop of flowers (Taylor 1964; Wien & Tayo 1979; Tamò et al. 1993b; van de Klashorst & Tamò 1995). Reduced pod set could be linked to increased thrips abundance, particularly larvae, in most cases. However, high initial flower numbers did not necessarily lead to high pod numbers. This was explained by the time and duration of thrips attacks as well as the natural flower shedding of cowpea, which can reach levels of up to 88% (Rachie & Roberts 1974; Wien & Summerfield 1984). Whereas early thrips attacks generally reduced flower numbers (leading to shedding of flower buds), delayed but high thrips numbers could have caused flowers to drop after they had been counted. This could explain the often-occurring discrepancy between high flower numbers and low pod numbers thereafter. Ojehomon (1968) found that the number of flowers that are naturally shed by the plant increased with the total number of open flowers per plant. Summerfield & Roberts (1983) and Summerfield et al. (1983) observed that only the first flowers contribute significantly to yields, which made it very difficult to interpret the implications of the total number of flowers produced per plant. The results show that lower flower numbers or pod set were not generally linked to higher thrips abundance, which indicates the interaction with other factors in addition to natural flower shedding, like soil fertility and vegetative growth, which both depend on the soil conditions. Many cases were observed where higher pod set occurred in spite of comparatively more thrips numbers. Higher vigor of the plants, based on particular soil and climatic conditions, could have led to an increased carrying capacity of plants (Tamò et al. 1993b), which enabled them to compensate better for losses through pests (Wien & Tayo 1979). In addition to pod numbers, pod weight and seed numbers account for about 83% of total cowpea yield (Janoria & Ali 1970), and are negatively correlated with pod numbers (Rachie & Roberts 1974). Low pod weights were linked to increased pest attack, which resulted in

flower shedding and compensatory growth of plants. The theoretically indefinite flower production of cowpea before it dies (Ojehomon 1968) led to an increased proportion of underdeveloped pods that dried up prematurely or had not ripened by harvest.

This study showed that thrips are indeed among the most important factors that determine final yields of cowpea. However, due to the various interactions that influence thrips abundance and their impact on plant health, it was difficult to explain yield by considering the impact of main factors alone. Whereas NPK application exerted influence on the whole complex, mulch never did appear to influence yields directly. Preceding conclusions (Chapters 2, 3, 4, 5) suggested that mulch was not considered to be a factor with significant influence on the system, and thus was not expected to influence yields, either.

Cowpea yield depends on several factors, which themselves interact. The estimation of yield of cowpea proves to be difficult and cannot be solved by following just one approach. The use of mulch in the given quantities did not have any detectable beneficial effect on cowpea yields under the short-term conditions of these trials. NPK as a means to instantly improve soil fertility was nevertheless not appropriate for increasing yields. Its positive effect on vegetative plant growth and pest abundance, which occurred to the detriment of generative organs, could not be compensated for by higher yields in general. The higher vigor of plants was at least partially opposed by negative NPK effects. A combined approach is suggested, an approach that uses mulch as a means to increase soil fertility in the long term and avoids periods of known maximums of pest populations. If chemical fertilizer is to be used, it might better be applied to crops preceding cowpea, as the cowpea will still benefit as a result of a residual carry-over effect.

7 Wild host plants around cowpea fields: Their capacity to stimulate pests' migration into adjacent cultivated fields and possible sites for aestivation during absence of cowpea

ABSTRACT Cultivation of cowpea, *Vigna unguiculata* (L.) Walp. (Leguminosae), is strongly influenced by the presence of alternative wild host plants, which harbor pests as well as antagonists due to the various benefits they provide for these insects. Both pests *Maruca vitrata* F. (Lepidoptera. Pyralidae) and *Megalurothrips sjostedti* Trybom (Thysanoptera: Thripidae) maintain a permanent population throughout the year without diapause while switching successfully among a wide range of different species. Flower samples were taken of all plants encountered in the vicinity of cowpea fields that might serve as hosts to these two pests. Flowers collected in the adjacent cowpea fields, served as comparison for population dynamics to be studied in wild and cultivated hosts. Pest monitoring in flowers of wild host plants continued throughout the year between March 1995 and August 1997, covering rainy and dry seasons in three regions of Benin. *M. vitrata* was rarely encountered in wild hosts where overall few larvae were collected. Results for *M. sjostedti* showed that pest abundance was generally low when no cowpea was present, which was the case in dry seasons. As soon as cowpea produced the first organs where adults of *M. sjostedti* could feed and oviposit, adult numbers in wild hosts in the vicinity of cowpea increased in parallel. This was mainly explained by increasing emigration from cowpea when feeding and oviposition sites became scarce. The response of larval numbers in alternative hosts was generally weak suggesting a higher suitability of cowpea, where oviposition primarily took place. As cowpea flowers aged or the plants ceased flowering, thrips populations decreased in both cowpea and wild hosts, indicating that the availability of resources was the basic requirement for high populations. Comparing parasitism on *M. vitrata* and *M. sjostedti* between wild hosts and cowpea, mortalities of *M. vitrata* larvae due to parasitoids were generally higher in cowpea. This was ascribed to a higher diversity of parasitoid species, the cumulative success across species being more favorable in cowpea. The single parasitoid that attacks larvae of *M. sjostedti* resulted in overall low parasitism rates but was more successful in wild host plants. The limited recognition of cowpea as host of *M. sjostedti* and a probably higher affinity to other thrips' species is discussed.

Polyphagous pests like the two under study rely on a wide range of host plants, cultivated or occurring naturally that alternate throughout the year. The sustenance of a permanent population without diapause, which does not exist in these two pests (Taylor 1967; Lewis 1973), depends principally on a successful host plant switching (Ananthakrishnan & Gopichandran 1993; Arodokoun 1996). Van Emden (1981) stated that natural vegetation could favor polyphagous pests while offering many different feeding and oviposition sites. This was confirmed by Way & Heong (1994), who found that increased biodiversity can also increase attacks by pests. Ofuya (1989) as well as Ezueh & Amusan (1988) agreed that the presence of weeds in or

around cowpea plots increased the abundance of and damage by of *Maruca vitrata* and *Megalurothrips sjostedti*. They attributed these results to a provision of more suitable resting sites. The importance of alternative hosts when cowpea is not present was discussed by Taylor (1978), Way & Cammell (1981), Tamò (1991) and van de Klashorst & Tamò (1995), who agreed upon the capability of both pests to maintain a permanent population throughout the year.

As far as antagonists in general and parasitoids of both pests are concerned, natural vegetation is crucial for the survival of their populations in the same way. The availability of alternative prey in absence of the target phytophage (van Emden & Williams 1974; van Emden 1990; van Driesche & Bellows 1996) and additional feeding sites, e.g., pollen and humidity (Powell 1986; Altieri et al. 1993), or the influence of wild species on antagonists' fecundity (Grijpma & Belde 1990), rate of emergence (Parra et al. 1990), and their parasitization rate (Liu et al. 1994; Arodokoun 1996), basically determine the overall impact these antagonists may have on pest populations.

This study intends to clarify the potential of exterior pest pressure on cowpea (Ezueh & Amusan 1988) and to compare antagonists' impact on pests to which they might be exposed differently due to wild or cultivated habitat structure. Apart from studies by Arodokoun (1996), who concurrently compared dynamics of *M. vitrata* and its antagonists in cowpea and *P. santalinoides* as wild host, comparable approaches were not found in literature. Hence, the following design of simultaneous comparison of the cultivated and several wild host species, covering both pests and their antagonists, allows new insight into a highly complex system of multitrophic interactions.

Materials and Methods

All sampling activities were carried out in weekly intervals throughout the year (from March 1995 to August 1997) in the three regions Tokpa/Ayou, Lema, and IITA. While cowpea was cultivated two times per year during rainy seasons, sampling in wild host plants continued during dry seasons. Around each replication (block) to which cowpea was assigned, roughly between 7 and 30 hectares were covered by intensive screening of all potential candidates that could be expected to serve as an alternative food source for the pests under study. Right after harvesting was completed in cowpea fields, host plant sampling "frames" (each block with its corresponding wild host plant environment) were moved to new sites to be cultivated the following season. The two sampling cycles in wild host plants therefore consisted of two different time scales: the long cycle (December to July) covered the long dry season, overlapping the first growing season, and the shorter cycle (August to November) filled the dry spell between the two rainy seasons, overlapping the second growing season. Wild plants were sampled systematically, guided by already known host plants of the two pests (Taylor 1978; van de Klashorst & Tamò 1995; Arodokoun 1996), mostly belonging to the family of *Fa-*

baceae. Intensive screening revealed additional hosts, including families other than *Fabaceae*. Altogether, 60 different species from 42 different genera out of 12 families were sampled, yielding 9 potential hosts for *M. vitrata* and 45 for *M. sjostedti* (Appendix). Plant material was checked using Berhaut (1967, 1975, 1976), de Souza (1988), and GTZ (1984), and partly assisted by Houngnon (pers. comm.). As potential host plants for *M. sjostedti,* all plants were considered from which larvae were isolated indicating a suitability to produce offspring on these plants.

Thus, the parallel sampling of cultivated cowpea and naturally occurring alternative host plants during rainy seasons allowed direct monitoring of migration of pests from their aestivation sites into cowpea. As a further step, parasitization rates in these alternative sources were monitored in parallel. This was an attempt to compare antagonists' impact on pests to which they might be exposed differently due to wild or cultivated habitat structure. This approach aimed at clarifying the potential of exterior pest pressure on cowpea (Ezueh & Amusan 1988; Ofuya 1989) by comparing regionally varying abundance levels in wild hosts to those of cowpea. Moreover, an explanation of time dependent patterns of host plants between regions (Arodokoun 1996) was sought to account for different assumptions in cowpea cultivation.

Taking into account a more sparse population in wild hosts, the sample size was increased from 20 to 50 flowers per plant species (Tamò, pers. comm.). For the long dry season in particular, it turned out to be important to increase the chance of encountering pests in flowers. Since the wild hosts serve mainly as aestivation site during this period of the year, pests maintain their populations on a lower level (Taylor 1967). The organs were dissected in the laboratory, and thrips (following Palmer 1990), the pod borer (following Taylor 1967), and antagonists were identified (Goergen, pers. comm.) and counted under the binocular. Means of insects per 50 flowers served as responses, which were reported on a per-flower basis. Since cowpea flowers were collected in a sample size of 20, the insect counts per 20 flowers were extrapolated to 50 flowers to allow comparison of insect abundance between cowpea and wild hosts. Parasitism in flowers was studied using exactly the same methods as in cowpea (Chapter 3). Some rare species revealed pods to be investigated. However, tentative sampling gave no impression of suitability of these organs, which is why the focus was on flowers.

The figures presented for comparative dynamics of pests (Figs. 7.1.-7.16.) sometimes contain cultivated crops that do not belong to the group of wild hosts. For a more complete design, they were included since as alternative hosts they also contributed with their presence in neighboring fields to the maintenance of the pest population.

The weekly change of flower abundance on host plants and the irregular distribution of these trees, shrubs and herbs created its own distinct pattern. Furthermore, the natural bias of host plant distribution due to soilborne influences (index plants) coincided with limited alternatives of locally available, suitable fields for experimentation. Any attempt of randomization turned out to be difficult. The location of plants was known better after some weeks of sampling and flower collection was guided by chance during walks through the area. Bias probably

was reduced the longer the distribution pattern of host plants was known. No effort was made to estimate flower densities in the host plants, and relative pest densities per host plant were not accounted for, either. Dissection of flowers as well as counting of insects in the laboratory was done in the same way as for cowpea (Chapter 3).

The generally patchy distribution of wild hosts as well as their sometimes rare or unique occurrence did not permit statistical analysis. Hence, direct comparison of pest abundance and parasitism levels in a descriptive way was used to draw conclusions. This chapter aims at complementing findings in cowpea, the principal target of this study, by emphasizing the necessity of an environmental dimension, which offers a complementary powerful interpretation tool.

The exact description of experimental sites and the research design, auxiliary data like climate and soil properties, and a detailed description of the statistical approach, which is of less importance in this chapter, were discussed completely in Chapter 1 and may assist in further understanding.

Results

Population dynamics in flowers

Maruca vitrata

During a sampling period from March 1995 to August 1997, larvae of *M. vitrata* were found in nine alternative host plants apart from cowpea (Table 7.1.). They could rarely be collected during consecutive sampling weeks although most of these plants were monitored almost continuously. The most important plant among these was *Dolichos africanus*, which revealed a maximum of 26 larvae per 50 flowers during one sampling event. *Tephrosia candida*, *Cajanus cajan,* and *Tephrosia bracteolata* followed on lower maximum numbers. Single larvae collections in the remaining plants have to be regarded as sporadic results and do not suggest preference for these plants. Uniquely *D. africanus* was considered as possibly contributing to an increase in population of *M. vitrata* since its high larval numbers in flowers coincided with about the same levels in cowpea at DAP 49 in season II/96 in Lema (Fig. 7.1.). For better comparison, larval numbers in cowpea were extrapolated usually from 20 flowers to the 50 flowers sampled in alternative host plants. A small tree of *D. africanus* was found flowering at DAP 49 and could be monitored during six consecutive weeks in parallel with cowpea. Both profiles decreased after DAP 49 but this was very sharp in cowpea while descending protractedly in *D. africanus*. Three weeks after the maximum population had collapsed to zero. *Vigna ambacensis* and *Erythrinia senegalensis* revealed single larval counts during the same season, but they were of no importance for the population.

Megalurothrips sjostedti

Tokpa/Ayou

First season (I/95)

At the time of sowing of cowpea fields, no plant of importance was found flowering in the neighborhood of the plots (Fig. 7.2.). Flowers of *Asystasia gangetica* did not reach more than 1.1 adults per flower and remained constant over several weeks, whereas the number of larvae in the same plant remained close to zero. Levels for *Carpolobia lutea* and *Physalis angulata* were of no importance. *Morinda lucida* always yielded very low counts. The initially higher numbers of adults in *C. cajan* dropped later on, before flowering of the available shrubs ceased weeks before sowing. An assessment of larval numbers indicated that the generally few organisms that were found did not point to a stable population in any of the plants sampled during this season. Sampling in alternative host plants did not continue after DAP 42 due to time constraints caused by exercises in cowpea.

Second season (II/95)

During the weeks before and after sowing, no considerable population levels were found in the plants neighboring the cowpea fields (Fig. 7.3.). *P. angulata* and *A. gangetica* once counted more than one adult per flower. Populations in *C. cajan* remained low until DAP 35, when, after a first peak and a following setback, adult numbers increased remarkably at DAP 49. The same happened for *Centrosema pubescens*, which started flowering around DAP 21 and strongly rose in adult numbers after DAP 42. This happened in parallel with first thrips counts in shoot tips and flower buds of cowpea, which showed an increasing trend for adults as well. Larval numbers remained below one organism per flower except for *C. pubescens*, where numbers increased after DAP 42. No reaction was observed for larvae in *C. cajan* due to increases of adults' numbers in the same plants and in cowpea. Sampling in alternative hosts was suspended after DAP 49 due to time constraints.

Third season (I/96)

The only plant of major importance was *C. pubescens* (Fig. 7.4.). For several months, a permanent population consisting of adults and larvae was found in flowers at a relatively stable level. Weeks before sowing of cowpea, the population strongly decreased in parallel with an increase in rainfall and decreasing flower densities. Two weeks before sowing the population sharply increased and reached its peak at DAP 0, the day of sowing of cowpea. While flower production in *C. pubescens* decreased, the population dropped slightly when the first sampling

in cowpea was started. An adjacent filed of groundnuts flowered weeks before cowpea was sown and showed similar thrips dynamics to *C. pubescens* for larvae and adults. At the end of the year 1995, *A. gangetica* and *Ipomoea involucrata* recorded more than one adult per flower and dropped to lower levels weeks after. However, *A. gangetica* constantly recorded adults during these months, its population collapsing many weeks before cowpea was sown. *M. lucida* revealed adults at some events without any importance. Larvae principally were found in *C. pubescens* and the adjacent groundnut field. At DAP 28, first sampling in shoot tips of cowpea recorded higher levels for larvae than for adults. One week later when flowering started in cowpea, levels for larvae and adults were lower in flower buds but already relatively high in flowers, where more adults were found. Sampling in wild host plants was suspended after DAP 49 in favor of exercises to be done in cowpea.

Fourth season (II/96)

Three plant species were of major importance throughout the entire cropping season of cowpea, *C. cajan*, *C. pubescens,* and *Cassia hirsuta* (Fig. 7.5.). In parallel with the steep increase of adults' population in cowpea towards DAP 56, which represented the peak of flowering (Chapter 2), populations rose for all three wild plant species as well. Whereas cowpea reached population levels of 106 and 110 adults per flower at DAPs 56 and 63, the peak in *C. cajan* recorded 23 adults at DAP 63. The adult peak in alternative host plants occurred one week after the maximum in cowpea. Larval abundance in alternative hosts was lower for *C. cajan* and *C. hirsuta*, but about the same for *C. pubescens*. Larvae increased to their peak for *C. cajan* and their first maximum in *C. pubescens* one week later than the peak for adults. This pattern was therefore the same as in cowpea between adults and larvae. While thrips numbers dropped in cowpea after DAP 70, their numbers increased again in the three alternative hosts after DAP 77. Larval numbers in *C. hirsuta* in general were of low importance.

Fifth season (I/97)

At the time of cowpea cultivation, no important populations of thrips were found in the neighborhood (Fig. 7.6.). During a short period, flowers of *Lonchocarpus cyanescens* responded to thrips levels in cowpea, which peaked with 52 larvae per flower one week after wild hosts. Populations in *A. gangetica* also increased slightly after thrips numbers peaked in cowpea. Larvae were found in alternative hosts in some exceptional cases only. Months before cowpea was sown, *C. pubescens* revealed a permanent population of thrips with changing densities over several months but after flowering ceased for this plant, no other source of thrips hibernation was found for a long time.

Lema

First season (I/95)

Two alternative host plants were monitored during several months of screening: trees of *M. lucida* and *A. laxiflora* (Fig. 7.7.). The area was burned during the long dry season. Whereas *M. lucida* revealed some few adults following a short and moderate increase of population in *Afrormosia laxiflora,* the latter plant showed a sharp peak for larvae that lasted four weeks before flowering ceased completely. This was two weeks before cowpea was sown. Sampling in alternative host plants was suspended after DAP 42 in favor of exercises to be followed in cowpea.

Second season (II/95)

When the site was changed for a second cowpea cultivation, *T. bracteolata* was found already flowering (Fig. 7.8.). Initially low thrips numbers steadily increased towards DAP 35 and peaked with 40 larvae and 17 adults per flower. Larvae dropped thereafter whereas adults increased again after a setback at DAP 42. *Tephrosia platycarpa* started flowering weeks later and rapidly increased its population close to levels of *T. bracteolata*. *Cochlospermum planchoni* started with zero levels at DAPs 21 and 28, after which adults rapidly augmented their numbers parallel to the onset of first sampling in cowpea. At DAP 49, which was the flowering peak of cowpea (Chapter 2), *C. planchoni* counted 52 adults while 68 adults per flower were found in cowpea. An increase for larvae in *C. planchoni* happened one week after the one for adults and remained at lower levels. In addition, plants such as *V. ambacensis, Vigna reticulata,* and *E. senegalensis* contributed to an increasing population to a moderate extent. This was especially true for adults. During their peaks, *T. bracteolata* and *T. platycarpa* produced more larvae than adults. Sampling in alternative hosts was not continued after DAP 49 due to exercises to be done in cowpea.

Third season (I/96)

After DAP 7, thrips were no longer found in alternative host plants (Fig. 7.9.). Two weeks before the sowing date for cowpea, *A. laxiflora* had its short flowering period, which ceased after DAP 7. Moderate levels of adults and larvae were found in this species. Months before, flowers of *C. planchoni* were found during some weeks with constantly decreasing thrips levels. *V. ambacensis* showed similar patterns with fewer numbers of thrips. After two months when no important host plant appeared to be flowering, *Trichilia emetica* was found with already high larval and slightly lower adult numbers, which decreased constantly towards the end of its flowering cycle. *M. lucida* was monitored during the months, most of the time with levels close to zero. A short increase occurred in late April right before flowering ceased.

Fourth season (II/96)

This season was marked with a high number of potential alternative host plants in the neighborhood of cowpea (Fig. 7.10.). *C. planchoni*, *T. bracteolata*, *T. platycarpa*, *D. africanus*, and *E. senegalensis* were the plants of major importance that kept a permanent population during several weeks. *C. planchoni* and *D. africanus* reached highest levels with 42 and 47 adults per flower, respectively, during their maximum. When the flower peak in cowpea occurred at DAP 49 (Chapter 2), 100 adults and 37 larvae per flower were counted. These were 47 adults for *D. africanus*, 18 for *T. bracteolata*, and 5 for *T. platycarpa*. Larvae recorded on the same sampling day were 9 organisms for *T. bracteolata*, 5 for *T. platycarpa*, and 6 for *D. africanus*. Larval populations in *T. bracteolata* and *T. platycarpa* peaked at DAP 35, with maximums of 18 and 11 organisms per flower, respectively. *D. africanus* marked its maximum larval abundance of 12 at DAP 56, one week after the flowering peak in cowpea. As for adults, their abundance appeared to increase in parallel for alternative host plants and cowpea, and then also decreased simultaneously. For larvae, this pattern started two weeks earlier for *T. bracteolata* and *T. platycarpa*. At the end of the season when thrips abundance dropped in cowpea, the population in alternative host plants decreased considerably, too. During the season, thrips' numbers in cowpea were always superior to those recorded in alternative hosts except for larvae at DAP 42, when *T. bracteolata* revealed more than double the number per flower.

Fifth season (I/97)

In the dry season months before the cropping season started, moderate thrips numbers were maintained in *Pterocarpus erinaceus*, *Phaseolus lunatus*, *Vitellaria paradoxa* (= *Butyrospermum parkii*), and *T. emetica* (Fig. 7.11.). Higher adult numbers occurred early in the dry season in *C. planchoni*, which ceased flowering after three sampling weeks, two of which were without thrips counts. An interruption of flowering occurred later on partly due to local bush fires. With the beginning or the cowpea cropping season (DAP 0), *Lonchocarpus sericeus* and *T. bracteolata* were important for thrips populations. *L. sericeus* increased in thrips abundance right after sowing and dropped after a total of five weeks of flowering. *T. bracteolata* increased in population when cowpea started flowering at DAP 42. The first sampling in cowpea flowers at DAP 42 revealed already very high numbers of larvae (37 larvae flower^{-1}) and adults per flower (50). On the same day *T. bracteolata* yielded 53 larvae and 24 adults per flower. Weeks after cowpea had been harvested, thrips numbers remained relatively high in *T. bracteolata* when its main flowering period began. As *T. platycarpa* started flowering in early October, adult abundance in *T. bracteolata* increased again when in parallel thrips levels in *T. platycarpa* rose steeply.

IITA

First season (I/95)

During the dry season, thrips were maintained in *Tephrosia candida*, which served as an intercrop in neighboring fields and to a lesser extent in *C. cajan* (Fig. 7.12.). A wave-like abundance pattern occurred, which sharply peaked for adults at the date of sowing of cowpea. The adult population collapsed again thereafter. With the increasing size of cowpea plants, thrips' numbers rose again in both alternative host plants when *C. cajan* ceased flowering. Sampling in alternative hosts was suspended after DAP 35 due to the start of exercises in cowpea.

Second season (II/95)

Alternative host plants, such as *T. candida*, *T. bracteolata*, *C. pubescens,* and, during their short flowering period, *Cassia occidentalis* and *Pterocarpus tetragonolobus,* were the most important species during this season (Fig. 7.13.). Thrips reproduction was low in *C. pubescens*. Generally stable levels started increasing for adults in *T. candida*, *T. bracteolata*, and *C. pubescens* and for larvae in *T. bracteolata* when cowpea gained in size at DAP 35. On this basis, larval numbers in cowpea increased 20-fold and adults almost 4-fold in flower buds from DAP 42 to DAP 49. At DAP 49, the flowering peak of cowpea, 43 larvae and 97 adults per flower were counted. The same day, flowers of *T. bracteolata* revealed 6 larvae and 86 adults per flower. Time constraints did not allow sampling after DAP 49 in alternative host plants.

Third season (I/96)

T. candida maintained relatively high thrips levels at the beginning of the long dry season but the field was cleared later (Fig. 7.14.). *C. pubescens* flowered during some weeks in parallel and contributed moderately to the population. *T. bracteolata* was found flowering one time but resulted in low levels only. The following weeks before and after sowing of cowpea, only *A. gangetica* was found to keep some few adults during four weeks, although it was present during many months with counts close to zero. At DAP 49, no thrips were found around the cowpea fields. Thrips numbers in cowpea were relatively low the same day, which was its peak of flowering (Chapter 2). Sampling in wild hosts was suspended thereafter.

Fourth season (II/96)

T. candida ceased flowering at the beginning of the cowpea growing season (Fig. 7.15.). This was the time when *T. bracteolata* started its flowering period, which lasted until one week before cowpea reached its flower maximum at DAP 56. Whereas adult numbers increased in parallel to the growth of cowpea plants but remained at lower levels, larval abundance was

temporarily moderate at DAPs 28 and 35. One week after cowpea was sown, flowers of *C. pubescens* appeared. At the time when cowpea plants had reached a stage that allowed sampling of shoot tips (DAP 42), abundance of larvae and adults started rising in *C. pubescens*. The profile was similar to the shape of curves for cowpea and decreased together with thrips numbers in cowpea flowers. *Dolichos argentum* appeared flowering during a short period after the maximum in cowpea and reacted positively to its high thrips numbers. Thrips abundance was always more elevated in cowpea flowers than in alternative host plants.

Fifth season (I/97)

Before the cowpea season started, low to moderate levels of thrips were found in *C. pubescens* and *T. candida* (Fig. 7.16.). The latter ceased flowering by the end of February and started again in August. *C. pubescens* stopped its flowering cycle in the second half of April. In early July, *C. occidentalis* was found flowering and once recorded moderate numbers of thrips right at the peak of flowering of cowpea at DAP 49 (Chapter 2). When *T. candida* started flowering anew, thrips levels remained comparatively low and decreased together with levels in cowpea. A short increase of larvae in *T. candida* at the end of the cowpea season (DAP 77) occurred in parallel with an again rising abundance of larvae and adults in cowpea. Except for *T. candida*, thrips numbers in cowpea were always superior to those in alternative host plants.

Parasitism in flowers

Maruca vitrata

During five seasons at IITA, 32 larvae were found in total that were assessed for parasitism in alternative host plants (Table 7.2.). Parasitism did not occur during this period. In Tokpa/Ayou, 29 larvae of *M. vitrata* were collected during five seasons in *C. pubescens* and *L. cyanescens*. The latter revealed three larvae only, out of which one was parasitized in season I/97 by *Phanerotoma leucobasis* Kriechbaumer (Hymenoptera: Braconidae). In Lema, parasitism was recorded during seasons II/95 and II/96 on *T. bracteolata*, *T. platycarpa,* and *D. africanus*. During one event in season II/95, four larvae were collected in *T. platycarpa,* where one parasitized larvae was found only. Within season II/96, three consecutive weeks yielded 93 larvae in *T. bracteolata* resulting in 18 that were parasitized. At DAP 35 in the same season 12 parasitized larvae were obtained from the 49 that were sampled in total. The 67 larvae found in *D. africanus* at DAP 56 yielded 10 parasitized larvae.

When plant species were pooled across seasons, both *T. bracteolata* and *T. platycarpa* were close to 20% parasitism mainly due to *Braunsia kriegeri* Enderlein (Hymenoptera: Braconidae) (Table 7.3.). *D. africanus* scored slightly lower and was parasitized exclusively by *P.*

leucobasis. Only three larvae were found in *L. cyanescens*, one of which was parasitized by *P. leucobasis*. In total, of all larvae found in plants with at least one-time parasitism during the whole sampling period, parasitism amounted to 18%. When all larvae were summed including those plants that never recorded parasitism, the overall level was 12.2%. *B. kriegeri* was the prevailing parasitoid.

A comparison of these findings to those in cowpea at IITA showed some parasitization events in cowpea whereas no attacks were detected in alternative host plants in season I/95, I/96, or II/96. A parasitization rate of 3.1% was recorded in cowpea for season I/95, and in season I/96 two events yielded 4.5 and 1.3, respectively. In season II/96, one larva was found in flowers in total. It was parasitized by *P. leucobasis*. At Lema, the assessment of cowpea revealed overall parasitism rates of 26% in season II/95 and 32 in II/96. No parasitized larvae were encountered during long dry seasons and the following early rainy seasons. Alternative host plants recorded no parasitism in *T. bracteolata* during season II/95 and 13% in *T. platycarpa*. In season II/96, this was 24 in *T. bracteolata*, 21 in *T. platycarpa* and 14 in *D. africanus*. Whereas larvae in *C. pubescens* in Tokpa/Ayou were not parasitized in season II/96, the level in cowpea was about 16%. *L. cyanescens* scored 33 on the average on three larvae across only two events in season I/97, when in turn the rate in cowpea was 3.4 for 1,817 larvae in total.

While no parasitism was found at IITA during the whole sampling period, the overall parasitization level was 1.6% in cowpea. Tokpa/Ayou recorded attacks in *L. cyanescens* only, with one parasitized larva out of three organisms (Table 7.3.). Including plants where *M. vitrata* was found without ever being parasitized, this dropped to 3.4%. Cowpea reached 3.8%. Lema accounted for a general mean of 18%, consisting of *T. bracteolata*, *T. platycarpa*, and *D. africanus*. The incorporation of all plants that showed no parasitism brought the calculation to 14.5%, and to 18.7 across seasons in cowpea. Across all regions and seasons, alternative host plants reached a mean of 12.2% (344 total larvae) whereas this was 11.1 (10,855 total larvae) in cowpea. However, levels in alternative hosts were based on comparatively few larvae and strongly biased through the high rate in *L. cyanescens* found in Tokpa/Ayou. The general pattern of regional dominance in Lema, compared with Tokpa/Ayou and IITA that was found in cowpea, applied in the same way for alternative host plants.

Megalurothrips sjostedti

Three plant species at IITA were targets of *Ceranisus menes* Walker (Hymenoptera: Eulophidae), the parasitoid of *M. sjostedti*. *C. cajan* and *C. pubescens* revealed once parasitism rates of 2.2% and 3.7, respectively (Table 7.4.). *T. candida* yielded parasitized larvae at the beginning of the first cowpea cropping season (I/95) but was sampled for a long time before without success in parasitism. The maximum level during this season was 4.6%. One year later in the dry season before season I/96, six consecutive weeks yielded parasitized larvae with a

peak of 20.2%. Whereas the parasitism levels were high when monitoring of *T. candida* was started, mortalities due to parasitism dropped during the following weeks to very low levels in February, when several events with no parasitism occurred. During both late cropping seasons and their preceding dry spells no parasitism occurred at all.

Many different alternative host plants in Lema were targeted by the parasitoid right before and during seasons II/96 and I/97. *E. senegalensis*, *L. sericeus,* and *P. erinaceus* yielded parasitized larvae during one event only, although being sampled more than one time. *P. erinaceus* recorded comparatively low levels. Thrips were found being parasitized once in *C. planchoni* in seasons II/96 and I/97, respectively. Low larval numbers were parasitized heavily in season II/96 but higher numbers in I/97 were attacked moderately. *D. africanus, Eriosema griseum*, *T. bracteolata,* and *T. platycarpa* resulted in parasitized larvae in season II/96 during several weeks with high parasitization rates at the beginning and remarkably decreasing levels in the following weeks. This always happened during the cropping seasons when cowpea was present in adjacent fields.

As for Tokpa/Ayou, *C. cajan* yielded one parasitized larva during one event in season II/96, resulting in a parasitization rate close to 1%. *L. cyanescens* and *L. sericeus* also revealed a few parasitized larvae at one sampling event, respectively, early in season I/97. Both parasitism levels were low. *C. pubescens* yielded parasitized larvae in the dry season before season I/96 and once at the end of season II/96, the rate for the latter event remaining below 1%. The highest score, which occurred in the dry season preceding season I/96, was 15.8%. This decreased later on.

For better comparison, parasitism rates were pooled across seasons within regions (Table 7.5.). All larvae found during the whole sampling period in these plants were assessed against the number of parasitized larvae. The total per region consists of the sum of larvae per region. The grand total is more than the sum of all totals since larvae were found in other plants that were never targets of parasitism. At IITA, *T. candida* remained low with about 3% only. *C. cajan* and *C. pubescens* did not reach 1%. Lema showed relatively high levels in *L. sericeus* – close to 30% – on comparatively few larvae. *C. planchoni* was above 20%, followed by *E. senegalensis* with 14.5. The remaining species scored below 10%, with *P. erinaceus* being lowest close to 1. The comparison of host plants in Tokpa/Ayou revealed that *L. cyanescens* recorded highest parasitism rates with 3.5% followed by *C. pubescens*, which reached half the parasitism levels on almost 10-fold higher larval numbers. One parasitized larva was found in *C. cajan* only. This was about the same rate that resulted at IITA. Parasitism rates of *C. pubescens* were more than eight times higher in Tokpa/Ayou than those at IITA. Lema revealed generally highest parasitization rates with 7.5% – more than threefold higher than the 2.2% at IITA and more than four times superior to the rates in Tokpa/Ayou.

Parasitism rates recorded in alternative host plants were also compared with those in cowpea. For season I/95 at IITA, cowpea reached parasitization rates of 1%, whereas *C. cajan* reached 0.5 and *T. candida* revealed 1.3 (Table 7.4.). When comparing within season I/96, *T.*

candida reached 7.9%, contrasting with 0.7 in cowpea. In season I/97, larvae in cowpea were parasitized in total at 0.2% and *C. pubescens* scored 0.4. Cowpea recorded 0.8% parasitism during season II/96 in Lema. *C. planchoni* reached 70.0%, *E. senegalensis* 15.9, *D. africanus* 8.0, *T. bracteolata* 7.3, *T. platycarpa* 5.3, and *E. griseum* 5.0. For season I/97, cowpea reached 6.9% compared with *L. sericeus* with 29.0, *C. planchoni* with 10.9, and *P. erinaceus* with 1.3, all of which yielded larvae only once. The parasitism rate in cowpea in Tokpa/Ayou was 2.8% for season I/96, contrasting with *C. pubescens* at 2.3. Season II/96 yielded overall parasitism of 0.6% for cowpea; the rate was 0.6 for *C. cajan* and 0.4 for *C. pubescens*. The 1.0% parasitism in cowpea in season I/97 was opposed by 3.0 in *C. pubescens* and 3.5 in *L. cyanescens*.

The regional distinction in parasitism rates for cowpea partly applied for alternative host plants. Lema revealed significantly highest parasitization levels compared with both other regions with 2.9% on the average in cowpea. This was 2.5-fold more in alternative hosts with 7.5%. If all plants were included wherever larvae were found without any sign of parasitism, the level still reached 7.0%. Those host plants without events of parasitism usually did not contribute with high larval numbers. Parasitism in Tokpa/Ayou for cowpea was lower at 1.1%. Alternative host plants recorded 1.7%. When the remaining non-parasitized species were included, the level dropped by 0.1%. IITA marked lowest levels for cowpea and yielded 0.3% parasitized larvae only. In alternative host plants, the rate was 2.1%, and dropped by 0.1 for all species together from which larvae were collected. Opposite to results for parasitism in cowpea indicating lowest rates at IITA, it was Tokpa/Ayou that recorded lower parasitism in alternative host plants compared with both other regions. However, except for some particularities within seasons, parasitoid impact on thrips larvae was considerably higher in wild host plants compared with the cultivated host, the cowpea, which was available temporarily.

Discussion

Population dynamics in flowers

Maruca vitrata

The few events where *M. vitrata* was encountered in wild host plants and the overall low numbers confirm the general impression from preceding chapters that *M. vitrata* was not considered important throughout the five sampling seasons and the respective dry seasons. Larval collections in wild hosts can be considered sporadic in terms of the number of sampling weeks and the events when larvae were found in samples (Table 7.1.). Except for *D. africanus*, where a high but short abundance was recorded, the other plants hosted very low population levels.

No signs were observed that cowpea cultivation led to subsequent increase in populations on the remaining alternative host plants. High larval abundance occurred in *D. africanus* in parallel to cowpea cultivation (Fig. 7.1.). During the first encounter of this small isolated tree, which flowered at this particular time, larval numbers were already at their maximum. It was not possible to gain insight into preceding population dynamics in this plant. However, the fact that the larval population in *D. africanus* declined as the population in cowpea dropped, indicates a strong influence of cowpea on this wild host. As larval numbers reached zero in cowpea, this occurred in *D. africanus* in parallel, despite the ongoing flowering in the wild host for another three weeks. It is likely that increasing pest pressure in cowpea led to emigration of adults into the available alternative host in the vicinity. This tree seemed to be more appropriate than other plants that were sampled, but resulted in rare events only. The decline in population in *D. africanus* suggests a reduced oviposition of adults, which can be seen in coincidence with aging flowers in this plant (flowering of this plant ceased at the end of November). A reduced supply of assimilates, particularly nitrogen, which was reported by Ojehomon (1968) and Summerfield et al. (1983) for late flowers of cowpea, might be a reason for reduced suitability for *M. vitrata* in *D. africanus*. However, the encounter of larvae in non-cultivated host plants at different times when cowpea was not present confirms the results of Taylor (1978) and Arodokoun (1996) that *M. vitrata* survives on wild hosts in the dry season.

Megalurothrips sjostedti

Tokpa/Ayou

First season (I/95)

No important alternative host plant was encountered in this season. *A. gangetica* maintained a very low adult population while the low numbers of larvae, which were found irregularly, suggested that this plant was basically used as a feeding site for adults. Although the presence of adults at the onset of cowpea cultivation might have facilitated the colonization of cowpea as mentioned by Taylor (1969) and Tamò et al. (1993a), the slow growth of thrips population in cowpea with a late peak at DAP 63 (Fig. 3.1.) (Chapter 3) did not suggest a considerable contribution to pest pressure in cowpea.

Second season (II/95)

Low populations of thrips were monitored in several wild hosts around the cowpea fields before cowpea was sown and during the first weeks of growth (Fig. 7.3.). The steep increase in adult populations in *C. cajan* and *C. pubescens* started as the first flower buds were sampled

in cowpea. Thrips were regularly found in shoot tips of cowpea. The appearance of shoot tips created oviposition sites for thrips, which subsequently emigrated into *C. cajan* early in the season. The rise in populations in wild hosts coincides with the appearance of flower buds and early flowers, which are known as preferred feeding and oviposition site for *M. sjostedti* (Tamò et al. 1993b). Since no larval increase occurred before the adult population growth, their increase is assumed to be the result of emigration from cowpea as pest pressure increased. The high number of adults in cowpea at DAP 63 probably indicates the high migration activity from and into cowpea. Larval abundance also rose in *C. pubescens* after DAP 42. This can be interpreted not only as evasion of population pressure in cowpea but also as a successful colonization of this host.

Third season (I/96)

C. pubescens maintained a moderate population for months. The first decline in populations was due to decreasing flower numbers in early April. In addition, precipitation started rising early in April, which together with scarcity of flowers in *C. pubescens* probably caused the population to collapse temporarily. A following increase in adult and larval populations possibly was a concentration effect of a newly growing population on sharply falling flower numbers. A few weeks after cowpea was sown, *C. pubescens* ceased flowering and no other alternative host remained. A week of strong precipitation after DAP 42 delayed a population peak of thrips in cowpea, which led to a late moderate peak of larvae and adults at DAPs 63 and 70. The scattered population in a declining *C. pubescens*, together with the heavy rains, was likely to limit the migration from the wild into the cultivated host.

Fourth season (II/96)

As soon as cowpea started flowering (DAP 49) (Fig. 7.5.), populations of adults in the wild hosts *C. cajan*, *C. pubescens*, and *C. hirsuta* were rising in parallel to those in cowpea. Since larval numbers in shoot tips and flower buds in cowpea were close to zero, the sharp increase in adult numbers in cowpea likely stemmed from movement out of wild hosts, which caused the initial infestation of cowpea (Taylor 1969; Tamò et al. 1993a). The increase in *C. pubescens* after DAP 49 was due to immigration by adults since almost no larvae were found in *C. pubescens* before DAP 63. The fact that all three wild species showed an increase in population at the same time proposes an emigration out of cowpea following increasing pest pressure. Higher infestation levels in cowpea compared with wild hosts present suggests that cowpea's suitability due to its uniformity and concentration of resources (e.g., flower buds, flowers) per unit was more favorable for thrips.

Fifth season (I/97)

After *C. pubescens* ceased flowering in March, there was a long gap when no alternative host plant was flowering. One week after the flower peak of cowpea, low adult numbers in *L. cyanescens* responded slightly, rising in numbers, too. Adults from cowpea presumably immigrated into *L. cyanescens,* temporarily leading to higher abundance. However, the short appearance of flowers and the low abundance of thrips in this wild host did not contribute to an important population in the neighborhood of the cowpea fields. Larval numbers in cowpea exceeded those of adults, thus indicating that the population developed within cowpea starting with low adult numbers.

Lema

First season (I/95)

Four weeks before cowpea was sown, a short and high larval peak occurred in *A. laxiflora*. Adults in the same species and in *M. lucida* hardly reacted and the whole population collapsed after flowering in *A. laxiflora* ceased. No other hosts were available to which adults could migrate. Low adult numbers were found during these weeks in *M. lucida* but the plant seemed not to be suitable for *M. sjostedti*. Thrips numbers in cowpea remained low as a result, as no considerable migration from host plants was expected. The higher proportion of larvae suggested that the population developed basically from within the cowpea field.

Second season (II/95)

Starting with very low thrips numbers per flower, *T. bracteolata* developed a high population of adults and particularly larvae as cowpea grew in size (Fig. 7.8.). A strong increase was observed during the weeks towards a peak at DAP 35. The levels dropped when the first shoot tips and flower buds were sampled in cowpea. The movement of adults into cowpea might have caused this drop in abundance of adults and also for larvae, since adults, which emigrate, may oviposit on cowpea rather than the wild host. Adults increased again towards DAP 49 when high adults' abundance was recorded in cowpea flowers. The increasing thrips population pressure is likely to have caused movement from cowpea back into wild hosts, which explains the rising population in *T. bracteolata*, *C. planchoni, E. senegalensis, V. ambacensis,* and *V. reticulata*. Larval numbers in cowpea remained relatively low since flower production in cowpea was scarce thus not favoring high oviposition.

Third season (I/96)

The last larvae in wild hosts were monitored at DAP 7 when *A. laxiflora* ceased flowering. Although in low abundance, adults found early shoot tips of cowpea on which they could develop and oviposit. Moderate levels were recorded early at DAP 42, and increased further. Since no alternative host plants were flowering in the vicinity, the population was assumed to have developed from within the cowpea field, although migration from outside the monitoring area by wind drift was not excluded.

Fourth season (II/96)

Because this was a late season, thrips levels in wild hosts were already at very high levels. These were populations that switched over from early season cowpea into available alternative hosts. A slight drop in populations, which occurred before newly sown cowpea reached the flowering stage, turned into an increase as soon as cowpea developed shoot tips and flower buds. Migration between the wild and the cultivated hosts was suggested as the origin of this increase. The use of larval numbers as an indicator for suitability of the host plant points to *T. bracteolata, T. platycarpa, D. africanus, C. planchoni,* and *E. senegalensis* as favorable hosts for thrips' colonization. Van Emden (1981) and Way & Heong (1994) noted that biodiversity and natural vegetation tend to enhance phytophagous pests and may lead to increased attacks. The high host plant diversity in this season, consisting of highly suitable hosts, stabilized thrips' populations at a very high level. As cowpea started aging and alternative host plants like *C. planchoni* and *D. africanus* reached the end of their flower period, the thrips population continuously decreased. Increasing scarcity of resources might have served as a signal, subsequently leading to a drop in population. Populations are maintained at generally low levels during the off-season, when no cowpea is available (Taylor 1967). For plants that approach the end of their flowering period, this signal probably consists of a change in the composition and amount of assimilates transported to flowers. Transport of assimilates is reduced the later flowers are set (Ojehomon 1968; Summerfield et al. 1983). This might also explain why pest abundance generally dropped at the end of cowpea seasons although flowers were still produced due to the semi-determinate growth type that was used.

Fifth season (I/97)

When *T. bracteolata* started flowering again shortly before cowpea was sown, moderate larval abundance led to an increase of adults two weeks later, which in turn was accompanied by a population increase in *L. sericeus*. The latter contributed very little to the population as its flowering period lasted only three weeks. At the time when cowpea set flower buds, the abundance of larvae and adults of thrips in *T. bracteolata* rose steeply. This was partly due to dropping flower numbers, which might have caused a concentration effect of a given population on a reduced quantity of resources. Another break in flowering of *T. bracteolata* occurred before

it started again with low flower numbers at end August. Because of higher larval numbers at this time compared with adults, the migration from cowpea into *T. bracteolata* was considered not the main source for thrips abundance in this wild host. It might rather have developed from remaining flowers where the population increased as another flowering flush started. As *T. bracteolata* entered its main flowering season in September, the population increased again, probably due to an increase of feeding sites since *T. platycarpa* started flowering at the same time.

IITA

First season (I/95)

The different peaks of thrips in *T. candida*, which occurred before cowpea was sown for this study, may have occurred in coincidence with other cowpea plots, which alternated almost permanently throughout the year. Since *T. candida* was flowering throughout the whole monitoring period, which started in March (Fig. 7.12.), this was not a function of varying flower numbers. After cowpea was sown for this study, abundance of thrips rose again in parallel. As *C. cajan* ceased flowering at DAP 14, *T. candida* remained the only alternative host. Due to its proximity to the cowpea plots, the first adults, which probably developed in early shoot tips, possibly started migrating into *T. candida* and established an increasing population. The parallel rise in larval numbers suggested this conclusion. Apart from these peaks over time, thrips abundance remained rather low in the wild host, confirming the corresponding statement of Taylor (1967).

Second season (II/95)

As cowpea grew in size, an increase in the population of adult thrips was observed in alternative host plants, in particular *T. candida*, *T. bracteolata*, and *C. pubescens*. A remarkable increase started after DAP 35, when shoot tips of cowpea became abundantly available. Shoot tips are the first sites of colonization of the cowpea plant (Tamò et al. 1993b). With the appearance of flower buds and flowers (Fig. 7.13.), which are more attractive than shoot tips for colonization of *M. sjostedti* (Tamò et al. 1993b), thrips' adult population reached very high levels. Although a slow increase in larval numbers was observed for *T. bracteolata* and *C. pubescens*, this was not the case in *T. candida*. Increased adult numbers were probably the result of emigration from cowpea, where increased population pressure led to scarcity of feeding and oviposition sites (Tamò & Baumgärtner 1993). Since oviposition did not immediately increase in wild hosts, they were possibly used by adults as additional feeding sites but oviposition basically took place in cowpea. The result was an extremely high larval abundance in cowpea flowers at DAP 49. Thrips abundance in cowpea was extremely high during this season, which

can be ascribed mainly to the diversity of alternative host plants (van Emden 1981; Way & Heong 1994).

Third season (I/96)

At the time when cowpea was sown, no alternative host plant was flowering at the IITA Station except for *A. gangetica*, but this was not considered important. Although these levels were very low, a slight increase of adults was observed in coincidence with the formation of shoot tips in cowpea. It is likely that some adults emigrated from cowpea while searching for alternative hosts, and *A. gangetica* was the only species available at that time. The increase in adult numbers in *A. gangetica* may be explained in part by a temporary decrease in flower numbers, which might have led to a concentration effect in the fewer remaining flowers.

Fourth season (II/96)

As feeding and oviposition sites in cowpea became available, an increase in thrips adults was observed in *T. bracteolata, C. pubescens,* and *D. argentum*. Growing population pressure in cowpea pushed adults to emigrate into *C. pubescens*, which was mainly used as alternative feeding site. This is indicated by comparatively more adults than larvae in flowers of *C. pubescens* (Fig. 7.15.). *D. argentum* served exclusively as feeding site for adults as only rare larvae were encountered, which did not suggest preference for oviposition. The main oviposition activity probably took place in cowpea since relatively more larvae were found than adults. In addition to adults that remained on cowpea for feeding and oviposition, those that left for alternative hosts might have switched between the wild and cultivated hosts while also contributing to a new generation in cowpea. When cowpea dropped in flower numbers towards the end of this particularly dry season (Table 3.6.), flowers became scarce. Although *C. pubescens* continued flowering, these resources were not sufficient to maintain the preceding large population and adult numbers dropped in cowpea as well as *C. pubescens*. Adult evasion from these plants was probably one reason. Since no important numbers of larvae had developed in *C. pubescens* and other species did not host them at all, the growth potential of thrips in wild hosts remained low due to the scarcity of resources and limited diversity (van Emden 1981; Way & Heong 1994), which did not favor a considerable population build-up outside cowpea.

Fifth season (I/97)

Cowpea was accompanied by a few species of alternative host plants. *C. occidentalis* revealed thrips presence in flowers only twice, which were shortly before and after peak abundance in cowpea. Some emigrating thrips adults might have used this plant sporadically as feeding site while also ovipositing on it. *T. candida* started flowering after the abundance peak of thrips in cowpea and might have served as a new site after cowpea became unsuitable due to

scarce and aging flowers. However, abundance in *T. candida* remained low and thrips probably migrated to other cowpea plots that were still available nearby.

Parasitism in flowers

Maruca vitrata

The basics of these studies on parasitism narrow down to the comparison between the wild host plants and the cowpea as a temporary cultivated host. Differences among the different species of wild hosts are mainly due to various patterns of suitability of these hosts for the parasitoid. These are basically interactions determined by the availability of alternative hosts or prey for antagonists (van Emden & Williams 1974; Powell 1986; van Driesche & Bellows 1996), the nutritive quality of alternative feeding sites (e.g., pollen) (van Emden 1990; Altieri et al. 1993), and the convenience or affinity of the host as influencing antagonists' fertility (Waage 1986a,b; Janssen et al. 1987; Kaiser & Pham-Delegue 1987; Grijpma & Belde 1990; Parra et al. 1990).

Monocultures demonstrated higher diversity and activity of natural enemies under experimental conditions attracted by a comparatively high prey and host population, but predators and parasites seemed to be more efficient in complex (polycultural) systems (Root 1973; Altieri et al. 1978). This basically applies for the comparison between alternative host plants and cowpea as investigated in this study. Arodokoun (1996) showed that the number of parasitoid species that oviposit into larvae of *M. vitrata* was higher in cowpea compared with wild hosts. According to Ehler (1985), total parasitism levels increase with the number of different parasitoids' species. This confirms that the higher mortalities in cowpea were the result of an increased diversity and thus improved activity of antagonists – regardless of their efficiency – that attack different instars of *M. vitrata*. The differences in parasitism between the wild and cultivated hosts among the three regions may be explained by the changing diversity of wild hosts in these regions. Lema showed a higher difference and resulted in overall more species considered as host plants for *M. vitrata* (Appendix). As antagonists strongly rely on alternative food sources (Powell 1986; Altieri et al. 1993), their abundance and thus parasitism level may change according to the availability of these food sources. Way & Heong (1994) stated that the distribution and abundance of insects in cultivated host plants depend in part on the insects' interaction over time with non-cultivated host plants.

Megalurothrips sjostedti

In contrast to findings on *M. vitrata*, parasitism rates on *M. sjostedti* were always higher in wild host plants. These results were based on a total of 79,211 thrips larvae, across three re-

gions and five seasons that were reared in the laboratory (68,690 larvae from cowpea, 10,521 larvae from wild host plants). In the case of *M. sjostedti,* only one parasitoid is recorded, *Ceranisus menes* (Tamò et al. 1993c). Its efficiency proved to be very low in cowpea (Tamò et al. 1997). Although pooled data across species of different wild hosts revealed comparatively low levels, they were higher than those observed in cowpea, indicating a much higher suitability of species like *L. sericeus, C. planchoni, T. candida, T. bracteolata, T. platycarpa,* and *E. senegalensis* (Table 7.5.). Isolated peaks of some of those species reached remarkably high mortality rates on thrips larvae. Adults of several hymenopteran species rely on wild flowers for the maturation of their eggs (van Emden 1990), and the perennial status of the wild vegetation favors the activity of parasitoids (Andow & Risch 1987). Tamò et al. (1997) assume that this parasitoid cannot effectively recognize cowpea as host for *M. sjostedti*. This probably explains the comparatively low rates in cowpea. Following the proposition by Root (1973) and Altieri et al. (1978), it is likely that *C. menes* requires a polycultural system to increase its efficiency. The phenomenon that mortality rates in season I/96 at IITA in *T. candida* and in season II/96 in Lema in *T. bracteolata, T. platycarpa* and also in *E. griseum* decreased over time was difficult to explain (Table 7.4.). As in the case of IITA, larvae were permanently available in moderate numbers and would have been a stable prey for *C. menes*. Tamò et al. (1993c) reflected that this parasitoid might be associated with other thrips species than *M. sjostedti* and be more attracted to *T. candida* than to other native plants.

This leaves room to speculate that although larvae of *M. sjostedti* are present, *C. menes* cannot maintain its population on this pest and in this host plant alone. Except for *C. cajan*, no other host plant was encountered in this season. Since none of the collected larvae in *C. cajan* were parasitized, its attractiveness was assumed low due to unknown reasons. No other thrips species was recorded in the same samples of *T. candida*. It is suspected that the parasitoid was lacking a particular prey or host plant at this time that could have served as suitable source to maintain its population. The parasitoids' population *in situ* decreased due to either emigration or an increased mortality caused by the lack of suitable prey. In the case of Lema, the decline was monitored during the time when cowpea was cultivated in the vicinity. One reason might be the distribution effect, which was suggested by van Emden (1981) and Speight (1983) to be due to an increased number of cultivated and wild host plants. In fact, the diversity of host plants in this particular season was rather high (Fig. 7.10.). Furthermore, larval abundance in several wild host plants and also in cowpea increased together, which again brings up the hypothesis of decreasing parasitism successes as larval abundance increases (Fig. 4.1.). This was discussed in Chapter 4.

Conclusions

This study shows that cowpea as a cultivated crop has a highly disturbing influence on the surrounding wild habitat. As Taylor (1967) observed, pest levels remain rather low during

cowpea off-season. These low populations aim at surviving over a resource-poor time when climatic conditions are difficult (e.g., dry season). A diapause, which would facilitate survival (Wolda 1988), is not known (Taylor 1967). As soon as cowpea in the vicinity reached a stage where feeding and oviposition became possible for *M. sjostedti* (e.g., shoot tips, flower buds, flowers), particularly adult abundance rose in wild hosts. This was mainly ascribed to early immigration into cowpea from the wild habitat (Taylor 1969; Tamò et al. 1993a) and a subsequent emigration back into the wild hosts as feeding and oviposition sites become scarce in cowpea (Tamò & Baumgärtner 1993). An increase of larvae in the wild host was not implied in general and guided the proposition that cowpea was more suitable for population growth of thrips. This was indicated by generally higher thrips abundance in cowpea, higher larval numbers, and thus greater oviposition.

In the case of *M. vitrata,* the unique incidence where cowpea cultivation coincided with flowering of *D. africanus* did not allow sound conclusions on mutual influences of wild and cultivated hosts. However, the nonexistence of a diapause for both pests was confirmed (Taylor 1967; Lewis 1973). No clear relationship was discovered between diversity of wild habitat or thrips abundance in these wild hosts and the subsequent thrips abundance in cowpea. This is additionally determined by interactions with climate (e.g., rainfall on migration) and soil fertility (e.g., potential of flower production, or compensation for losses). It was observed that the population build-up in cowpea was favored by higher species diversity or thrips abundance in alternative hosts.

The fact that migration of thrips and *M. vitrata* could not be measured directly but was assessed indirectly via population dynamics in the host plant community, was considered the bottleneck of the study. The direction of flow of migration could thus not be proven. However, the disturbing influence of cowpea as a monocrop on the surrounding habitat and the mechanisms of pest outbreaks from initially low levels was demonstrated.

In terms of parasitism, this approach did not allow an estimate of how far the presence of wild hosts has implications for parasitism in cowpea. In the case of *M. vitrata,* Arodokoun (1996) observed that a suitable alternative host plant in the vicinity increases the diversity and activity of parasitoids in cowpea. This led to overall more successes in cowpea, which sum across the number of species present (Ehler 1985). Although mortalities on thrips larvae bound to parasitism are much higher in the wild habitat, the indirect effect of alternative hosts must not be overlooked. Wild host plants are essential for many parasitoid species to maintain their population throughout the year (Levins & Wilson 1980; Risch et al. 1983; van Emden 1990; van Driesche & Bellows 1996). In the case of *C. menes*, which is considered very inefficient (Tamò et al. 1997)**,** it is probable that parasitism successes would be even lower in cowpea could this parasitoid not rely on alternative sources. Thrips leave cowpea flowers as population pressure increases (Tamò & Baumgärtner 1993) and are likely to switch back into neighboring wild host plants. The parasitoids' higher impact on thrips larvae in these hosts could, to a cer-

tain extent, reduce pest population increase in non-cultivated hosts and may thus diminish the pest potential that would threaten cowpea.

Because wild host plants may strengthen antagonist populations in various ways (van den Bosch & Telford 1964; Powell 1986; Altieri et al. 1993) (see also Chapter 4), but can also improve the framework for pests (van Emden 1981; Way & Heong 1994), it is difficult to decide whether the existence of wild host plants leads to an overall increase or decrease in pest abundance. The highly unpredictable nature of the interactions involved makes it difficult to arrive at a definitive judgement.

8 Conclusions and Recommendations

This study investigated the potential of mulch to influence the pest-antagonist complex in cowpea. The debate on mulch in the literature and the wide-ranging results about its impact on insects suggested that the underlying problem is indeed complex. A comparison of the different situations under which these authors obtained their results indicated that main factors like location, habitat, plant species, pest and antagonist species, climate, and probably methods differed considerably among these works. These different results can be ascribed basically to the interactions among those factors, which vary from setting to setting. The present study therefore was designed to cover three different climatic settings in very distinct habitats. Simplification, by reducing the whole approach to only one particular set-up, would probably have yielded simpler results, but these in fact could have been misleading.

The decision to apply repeated measures followed the intention to increase the reliability of the results. Instead of assessing spot samples only, trends were investigated to account for insect dynamics to a maximum extent. The tools for analysis that are known to be powerful (Potvin et al. 1990; Littell et al. 1996) indeed suggested statistically significant variation in many cases, where the biological relevance was limited or not important at all.

The hypothesis that mulch might influence the pest-antagonist complex was tested along basic stages of cowpea development in terms of plant physiology, pest population dynamics, parasitoid activity, damage and yield losses by *Maruca vitrata*, wild and cultivated plant communities, and the final yield of cowpea. None of the stages revealed an important change following the application of mulch. Mulch was part of a chain of factors (e.g., climate, habitat, soil fertility), with soil fertility generally dominating over the microclimatic effects brought about by organic soil cover. In view of the short-term objective, which focused on mechanical as well as physical properties of mulch, it is to be concluded that mulch is not an appropriate means for interfering with the pest-antagonist complex. It is conceivable that this would be different under long-term conditions, as antagonist populations generally follow the pest with delay (Hagen et al. 1976; van den Bosch et al. 1976). When mulch is used repeatedly on the same plot, the disturbing influence of clearing and weeding, which are done regularly, would be reduced and a build-up of populations of parasitoids and predators is likely (Goergen, pers. comm.). Studies would be needed to investigate the impact of long-term use of mulch on cowpea, and the respective change in soilborne fauna as well as micro-organisms.

Cowpea is known to be very tolerant towards stress factors like degraded soils or drought (Summerfield et al. 1983; Summerfield & Roberts 1983). The particular stresses that occurred during the five consecutive seasons were not accentuated in a way that strongly affected plant development. Mulch was thus not expected to remarkably improve growth conditions, which would have allowed a distinct development. Smaller variation probably was

masked by interactions with other factors. It can be assumed that the stimuli originating from plant development (i.e., onset of reproductive organs) were still the basic attractant to the insect. In seasons with high rainfall, the canopy closed completely due to the semi-determinate growth habit of the variety used and the visual stimuli that mulch might have exerted disappeared entirely. The strong population pressure from alternative host plants around cowpea fields represented a permanent migration between habitats as was shown in Chapter 7. Even if mulch would have favored the development of pest offspring that pupate in the soil litter (Taylor 1967; Rösingh 1980), the fluctuation between cowpea and wild hosts probably would have compensated for these differences. This was different in the case of NPK, since its application often resulted in a change of flower numbers or metabolism of the plant (Bentz et al. 1996; Mollema & Cole 1996), which could have favored the length of stay of adults on flowers, subsequently increasing oviposition.

As for parasitoids, the shelter effect decreased towards the end of the season. *Senna* and neem mulch (at IITA) decomposed very fast and left most of the soil bare at the time of harvest. Parasitoids, which reach the peak of their parasitization incidences toward the end of the growth period of the cultivated crop (Otieno et al. 1983), thus coincided with degrading shelter conditions. In the case of *C. menes*, this parasitoid seems to have other priorities than cowpea and *Megalurothrips sjostedti* as host (Tamò et al. 1993c). It is questionable whether mulch would exert the required stimulus to cause the parasitoid to accept a prey that probably is not the highest-ranking target in a plant, the recognition of which seems to be difficult for the parasitoid.

In the West African context, labor is a bottleneck and the means of transportation of large amounts of mulch material is not feasible for the small-scale farmer. From a technical point of view, the use of mulch would need convincing results to justify the efforts to be taken by the farmer. This did not occur in the present study. Mulch has excellent properties, the benefits of which are highly recommended. On the one side, soil fertility may stabilize requirements for certain predator species and soilborne micro-organisms, and on the other side, growth conditions are likely to increase plant vigor, which strengthens the capability to compensate partly for losses due to pest attacks. The major obstacle for any control measure remains the temporary character of the crop itself and the direct environment, which has to serve the short-term purpose. These conditions obviously favor pests, leaving antagonists underprivileged. A simplified approach to tackling the complex problem is likely to fail and has not yet shown promising results. A combined method that integrates the existing components of pest control might improve the chances of managing the existing severe pest problem more efficiently.

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Tables and Figures

Table 2.1. Soil sampling (raw data) during 5 growing seasons in Tokpa/Ayou, Lema and at IITA. Values are means of three blocks and 6 replications per block. Sampling was carried out weeks before sowing for cation exchange capacity (CEC), phosphate (P), pH, carbon (C), nitrogen (N), potassium (K) and magnesium (Mg). a) Upper stratum: 0-10 cm, high diameter core sampler, 5 samples per plot; b) Lower stratum: 10-60 cm, low diameter core sampler, 3 samples per plot.

a)	**Depth: 0-10 cm**	**CEC** (meq)	**P** (ppm)	**pH**	**C** (%)	**N** (%)	**K** (meq)	**Mg** (meq)
Season								
1	Tokpa/Ayou	8.91	9.30	6.38	1.48	0.12	0.44	1.49
	Lema	6.19	6.48	6.08	0.97	0.07	0.33	0.85
	IITA	5.64	7.35	4.92	1.17	0.08	0.18	1.36
2	Tokpa/Ayou	6.96	7.49	6.29	1.26	0.12	0.28	1.60
	Lema	4.14	5.25	5.97	0.59	0.05	0.31	0.72
	IITA	4.55	10.71	5.63	0.82	0.08	0.16	0.91
3	Tokpa/Ayou	7.54	7.21	6.15	1.35	0.10	0.22	2.27
	Lema	3.68	11.47	6.29	0.51	0.04	0.33	0.66
	IITA	4.48	8.18	5.66	0.93	0.07	0.22	1.43
4	Tokpa/Ayou	6.85	5.66	6.02	1.22	0.09	0.13	1.81
	Lema	3.58	5.62	5.84	0.45	0.04	0.25	0.49
	IITA	5.91	5.86	5.52	0.95	0.07	0.10	1.11
5	Tokpa/Ayou	7.14	5.20	5.68	1.49	0.11	0.16	2.38
	Lema	6.06	5.01	6.17	0.88	0.08	0.20	1.07
	IITA	5.29	7.33	4.64	0.95	0.09	0.15	1.26

b)	**Depth: 10-60 cm**	**CEC** (meq)	**P** (ppm)	**pH**	**C** (%)	**N** (%)	**K** (meq)	**Mg** (meq)
Season								
1	Tokpa/Ayou	5.52	2.89	5.97	0.62	0.06	0.22	0.99
	Lema	4.98	2.26	5.68	0.56	0.05	0.26	0.68
	IITA	3.69	3.46	4.74	0.60	0.05	0.14	0.98
2	Tokpa/Ayou	7.19	2.35	5.94	0.62	0.08	0.17	1.30
	Lema	4.21	1.89	5.97	0.32	0.04	0.18	0.63
	IITA	4.04	4.53	5.67	0.46	0.06	0.13	0.66
3	Tokpa/Ayou	6.65	1.65	5.53	0.62	0.07	0.21	1.36
	Lema	3.40	2.20	6.20	0.27	0.03	0.24	0.58
	IITA	4.50	1.95	5.62	0.41	0.05	0.14	0.94
4	Tokpa/Ayou	7.99	1.57	5.32	0.51	0.06	0.07	1.03
	Lema	3.47	2.12	5.78	0.21	0.03	0.23	0.41
	IITA	5.99	1.94	5.38	0.48	0.06	0.06	0.84
5	Tokpa/Ayou	6.71	2.19	4.82	0.69	0.08	0.09	1.44
	Lema	5.16	1.71	5.66	0.58	0.08	0.13	0.98
	IITA	5.32	2.95	4.48	0.57	0.08	0.11	1.09

Table 2.2. Precipitation (raw data) during 5 growing seasons in Tokpa/Ayou. Values are weekly sums (mm) and cumulative weekly sums (cum. sum) in mm of the preceding week and cover the period from one week before sowing until DAP 91. In earlier seasons measurement was suspended at DAP 70 and was extended during later seasons.

Season	I/95		II/95		I/96		II/96		I/97	
DAP	mm	cum. sum	mm	cum. sum	mm	cum. sum	mm	cum. sum	mm	cum. sum
0	54.6	54.6	7.3	7.3	18.5	18.5	4.6	4.6	39.4	39.4
7	4.2	58.8	19.1	26.5	18.8	37.3	7.3	11.9	66.1	105.5
14	41.0	99.7	0.7	27.2	23.0	60.3	15.5	27.4	65.0	170.5
21	25.7	125.5	6.8	34.0	47.1	107.4	1.4	28.8	119.5	290.0
28	81.4	206.9	12.4	46.4	48.9	156.3	23.0	51.8	36.2	326.2
35	4.9	211.8	4.9	51.2	111.5	267.8	49.6	101.4	34.1	360.3
42	0.0	211.8	83.3	134.5	18.1	285.9	12.2	113.6	73.5	433.8
49	21.8	233.6	36.9	171.4	98.0	383.9	62.4	176.0	34.2	468.0
56	9.9	243.4	40.1	211.5	27.6	411.5	27.9	203.9	41.4	509.4
63	5.4	248.9	0.0	211.5	0.4	411.9	1.4	205.3	1.3	510.7
70	33.5	282.4	0.0	211.5	61.7	473.6	0.0	205.3	78.2	588.9
77					1.7	475.3	0.0	205.3	0.0	588.9
84							0.0	205.3	3.8	592.7
91									0.0	592.7

Table 2.3. Daily mean temperatures (raw data) during 5 growing seasons in Tokpa/Ayou. Values are weekly means in °C of the preceding week and cover the period from one week before sowing until DAP 91. In earlier seasons measurement was suspended at DAP 70 and was extended during later seasons.

Season / DAP	I/95	II/95	I/96	II/96	I/97
0	27.1	26.9	27.0	-	24.0
7	27.0	26.8	25.9	25.3	25.7
14	27.2	26.4	26.6	25.1	25.3
21	26.4	27.1	25.9	24.9	24.9
28	26.1	26.8	26.4	25.6	25.2
35	26.0	28.0	26.5	25.9	25.9
42	25.6	26.7	25.7	26.6	24.9
49	26.1	26.6	25.3	25.1	24.8
56	25.3	26.3	25.5	26.4	25.1
63	25.5	27.9	25.4	27.5	25.2
70	25.5	27.0	24.2	26.1	24.1
77			25.1	27.1	24.4
84				27.4	24.8
91					25.8

Table 2.4. Precipitation (raw data) during 5 growing seasons in Lema. Values are weekly sums (mm) and cumulative weekly sums (cum. sum) in mm of the preceding week and cover the period from one week before sowing until DAP 91. In earlier seasons measurement was suspended at DAP 70 and was extended during later seasons.

Season	I/95		II/95		I/96		II/96		I/97	
DAP	mm	cum. sum	mm	cum. sum	mm	cum. sum	mm	cum. sum	mm	cum. sum
0	74.1	74.1	10.5	10.5	144.6	144.6	42.5	42.5	14.6	14.6
7	20.4	94.5	53.3	63.8	25.0	169.6	15.5	58.0	12.8	27.4
14	12.6	107.1	98.7	162.5	74.5	244.1	0.0	58.0	43.8	71.2
21	46.7	153.9	32.2	194.7	39.0	283.1	8.8	66.8	99.6	170.8
28	56.3	210.2	20.8	215.6	23.8	306.9	13.8	80.6	23.2	194.0
35	45.9	256.0	16.9	232.5	123.3	430.2	47.0	127.6	3.8	197.8
42	35.3	291.4	9.1	241.6	9.8	440.0	51.9	179.5	24.5	222.3
49	5.2	296.6	39.8	281.4	19.5	459.5	0.0	179.5	1.4	223.7
56	69.2	365.8	19.7	301.1	9.6	469.1	0.0	179.5	37.3	261.0
63	41.3	407.1	0.0	301.1	27.4	496.5	0.0	179.5	39.8	300.8
70	51.1	458.2	0.0	301.1	64.6	561.1	0.0	179.5	144.6	445.4
77					45.1	606.2	0.0	179.5	0.7	446.1
84							0.0	205.3	4.6	450.7
91									18.2	468.9

Table 2.5. Daily mean temperatures (raw data) during 5 growing seasons in Lema. Values are weekly means in °C of the preceding week and cover the period from one week before sowing until DAP 91. In earlier seasons measurement was suspended at DAP 70 and was extended during later seasons (- = problems with thermometer).

Season DAP	I/95	II/95	I/96	II/96	I/97
0	27.3	26.5	28.9	26.0	26.9
7	-	26.3	27.7	26.4	27.9
14	-	25.6	27.8	25.6	26.9
21	-	26.5	27.3	25.6	25.9
28	26.9	26.1	27.4	26.1	26.4
35	26.6	26.8	27.0	26.3	26.6
42	25.7	27.1	26.9	27.3	25.4
49	27.1	26.9	26.1	25.7	26.3
56	26.2	27.6	24.4	26.6	25.5
63	25.6	28.3	26.1	25.8	25.5
70	25.9	26.3	25.9	25.5	24.4
77			25.8	27.2	25.0
84					24.5
91					26.1

Table 2.6. Precipitation (raw data) during 5 growing seasons at IITA. Values are weekly sums (mm) and cumulative weekly sums (cum. sum) in mm of the preceding week and cover the period from one week before sowing until DAP 91. In earlier seasons measurement was suspended at DAP 70 and was extended during later seasons.

Season	I/95		II/95		I/96		II/96		I/97	
DAP	mm	cum. sum	mm	cum. sum	mm	cum. sum	mm	cum. sum	mm	Cum. sum
0	123.4	123.4	2.3	2.3	60.4	60.4	1.5	1.5	38.8	38.8
7	29.7	153.1	61.2	63.5	13.9	74.3	13.2	14.7	105.0	143.8
14	34.6	187.7	1.6	65.1	308.0	382.3	0.0	14.7	37.0	180.8
21	63.5	251.2	52.8	117.9	72.1	454.4	0.6	15.3	103.7	284.5
28	24.3	275.5	0.4	118.3	18.4	472.8	12.1	27.4	177.3	461.8
35	67.2	342.7	1.3	119.6	36.0	508.8	2.3	29.7	14.1	475.9
42	50.1	392.8	24.7	144.3	60.2	569.0	66.3	96.0	2.7	478.6
49	24.7	417.5	0.0	144.3	87.0	656.0	0.0	96.0	61.8	540.4
56	0.0	417.5	24.4	168.7	4.8	660.8	0.2	96.2	0.0	540.4
63	2.8	420.3	3.2	171.9	0.0	660.8	0.0	96.2	12.8	553.2
70	20.2	440.5	0.0	171.9	53.7	714.5	0.0	96.2	36.0	589.2
77					22.3	736.8	0.0	96.2	0.6	589.8
84									0.6	590.4
91									18.2	608.6

Table 2.7. Daily mean temperatures (raw data) during 5 growing seasons at IITA. Values are weekly means in °C of the preceding week and cover the period from one week before sowing until DAP 91. In earlier seasons measurement was suspended at DAP 70 and was extended during later seasons.

Season DAP	I/95	II/95	I/96	II/96	I/97
0	26.9	26.5	27.2	25.7	26.6
7	1.0	25.7	26.2	25.7	26.4
14	26.6	26.3	26.3	25.3	26.3
21	26.3	26.4	26.0	25.3	25.6
28	25.9	26.1	26.9	26.0	25.5
35	25.9	27.2	26.1	25.9	25.7
42	25.9	26.9	26.0	26.1	24.7
49	26.2	26.6	25.6	26.3	25.6
56	25.5	26.7	25.7	26.9	24.9
63	25.8	27.8	25.2	27.7	25.0
70	25.7	28.1	25.1	27.8	23.8
77			25.5	27.6	24.9
84					24.3
91					25.4

Table 2.8. Plant phenology: nodes per plant (mean per plant), comparison among 3 regions and 5 seasons. Values are means ± SEM ((√p + 3/8) transformed), region*season interaction, n = 1,350, $F_{(8,30)}$ = 3.4, $P < 0.01$.

Season / Region	I/95	II/95	I/96	II/96	I/97
IITA	6.7 ± 0.2a[1]A[2]	6.5 ± 0.3aB	5.5 ± 0.3aC	4.0 ± 0.3bD	5.9 ± 0.3cAB
Lema	6.6 ± 0.2aA	6.1 ± 0.2aB	5.2 ± 0.2aC	5.0 ± 0.2aD	6.7 ± 0.2bAB
Tokpa/Ayou	6.7 ± 0.2aA	5.9 ± 0.2aB	5.7 ± 0.2aC	4.8 ± 0.2abD	7.5 ± 0.2aAB

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 2.9. Plant phenology: flowers per plant (mean per plant), comparison among 3 regions and 5 seasons. Values are means ± SEM ((√p + 3/8) transformed), region*season interaction, n = 1,620, $F_{(8,30)}$ = 2.3, $P < 0.05$.

Season / Region	I/95	II/95	I/96	II/96	I/97
IITA	1.08 ± 0.06a[1]A[2]	1.06 ± 0.07aA	1.09 ± 0.06aA	0.80 ± 0.07aB	0.98 ± 0.06bB
Lema	0.92 ± 0.05bBC	0.95 ± 0.05aBC	1.20 ± 0.05aA	0.96 ± 0.05aC	1.03 ± 0.05bB
Tokpa/Ayou	1.15 ± 0.05aBC	0.98 ± 0.05aBC	1.18 ± 0.05aA	0.97 ± 0.05aC	1.16 ± 0.05aB

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 2.10. Plant phenology: pods per plant (mean of 10 plants), comparison among 3 regions and 5 seasons. Values are means ± SEM ((√p + 3/8) transformed), region*season interaction, n = 1,530, $F_{(8,30)}$ = 9.7, $P << 0.01$.

Season / Region	I/95	II/95	I/96	II/96	I/97
IITA	2.5 ± 0.18a[1]B[2]	1.5 ± 0.21aC	2.1 ± 0.18abB	1.2 ± 0.21bC	2.9 ± 0.21aA
Lema	1.1 ± 0.14bAD	1.1 ± 0.16aBD	2.0 ± 0.14bAE	1.7 ± 0.16aBC	1.6 ± 0.16bCE
Tokpa/Ayou	2.8 ± 0.14aB	1.3 ± 0.16aC	2.6 ± 0.14aB	1.4 ± 0.16abC	3.1 ± 0.16aA

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 3.1. Larvae of *M. vitrata* in flowers (mean number of larvae per flower), comparison among 3 regions and 5 seasons. Values are means ± SEM ((√p + 3/8) transformed), region*season interaction, n = 1,625, $F_{(8,30)} = 2.7$, $P < 0.05$.

Season	I/95	II/95	I/96	II/96	I/97
Region					
IITA	0.654 ± 0.013b[1]A[2]	0.619 ± 0.010bA	0.659 ± 0.010bA	0.615 ± 0.010bA	0.638 ± 0.009cA
Lema	0.688 ± 0.009aA	0.656 ± 0.008aA	0.696 ± 0.007aA	0.680 ± 0.007aA	0.673 ± 0.006aA
Tokpa/Ayou	0.684 ± 0.009abA	0.630 ± 0.008bA	0.655 ± 0.007bA	0.625 ± 0.007bA	0.668 ± 0.006bA

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 3.2. Larvae and adults of *M. sjostedti* in flowers (mean number of larvae and adults per flower), comparison among 3 regions and 5 seasons. Values are means ± SEM ((√p + 3/8) transformed), region*season interaction; a) Larvae, n = 1,625, $F_{(8,30)} = 10.8$, $P << 0.01$; b) Adults, $F_{(8,30)} = 12.8$, $P << 0.01$.

a) LARVAE

Season	I/95	II/95	I/96	II/96	I/97
Region					
IITA	4.0 ± 0.4a[1]BC[2]	5.0 ± 0.3aAC	3.3 ± 0.3aB	3.2 ± 0.3aB	2.4 ± 0.3bB
Lema	2.4 ± 0.3bB	2.5 ± 0.2bB	3.5 ± 0.2aA	3.2 ± 0.2aAB	3.7 ± 0.2aA
Tokpa/Ayou	3.5 ± 0.3aAB	3.8 ± 0.3bA	2.1 ± 0.2bC	3.6 ± 0.2aAB	3.0 ± 0.2bB

b) ADULTS

Season	I/95	II/95	I/96	II/96	I/97
Region					
IITA	4.2 ± 0.4aB	4.9 ± 0.4aA	3.4 ± 0.4aB	2.4 ± 0.4bA	2.3 ± 0.3bB
Lema	1.8 ± 0.3bB	3.3 ± 0.3bA	4.1 ± 0.3aB	5.1 ± 0.3aA	3.7 ± 0.3aB
Tokpa/Ayou	3.4 ± 0.3aB	3.9 ± 0.3bA	2.4 ± 0.3bB	4.8 ± 0.3aA	2.9 ± 0.3bB

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 3.3. Densities of larvae and adults of *M. sjostedti* in flowers (mean number of larvae and adults per flower counted the same day), comparison among 3 regions and 5 seasons. Values are means ± SEM (arcsine √p transformed); a) Larvae, region effect, n = 1,095, $F_{(2,30)} = 7.8$, $P < 0.01$, season effect, $F_{(4,30)} = 5.6$, $P < 0.01$; b) Adults, region*season interaction, $F_{(8,30)} = 5.2$, $P < 0.01$.

a) LARVAE

Season / Region	I/95	II/95	I/96	II/96	I/97
IITA	0.046 ± 0.007a[1]B[2]	0.067 ± 0.007aA	0.049 ± 0.007aAB	0.060 ± 0.008aAB	0.048 ± 0.008aAB
Lema	0.032 ± 0.006aBC	0.030 ± 0.005cC	0.030 ± 0.005bC	0.053 ± 0.006aA	0.047 ± 0.005aAB
Tokpa/Ayou	0.038 ± 0.006aBC	0.047 ± 0.006bAB	0.023 ± 0.006bC	0.056 ± 0.006aA	0.039 ± 0.005aB

b) ADULTS

Season / Region	I/95	II/95	I/96	II/96	I/97
IITA	0.043 ± 0.0072aB	0.063 ± 0.0060aA	0.045 ± 0.0067aAB	0.041 ± 0.0075cB	0.038 ± 0.0074aB
Lema	0.027 ± 0.0058aC	0.040 ± 0.0051bBC	0.039 ± 0.0051aBC	0.088 ± 0.0056aA	0.046 ± 0.0049aB
Tokpa/Ayou	0.037 ± 0.0056aBC	0.045 ± 0.0056bB	0.028 ± 0.0053aC	0.068 ± 0.0058bA	0.039 ± 0.0050aBC

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 3.4. Tokpa/Ayou, larvae of *M. vitrata* in flowers (mean number of larvae per flower), comparison among 5 seasons. Values are means ± SEM ((√p + 3/8) transformed), n = 623, $F_{(4,10)} = 12.2$, $P < 0.01$.

Season	I/95	II/95	I/96	II/96	I/97
Tokpa/Ayou	0.68 ± 0.008A[1]	0.63 ± 0.007C	0.65 ± 0.006B	0.62 ± 0.007C	0.67 ± 0.006AB

[1] Means followed by the same letter are not significantly different at $P \geq 0.05$.

Table 3.5. Tokpa/Ayou, numbers of larvae and adults of *M. sjostedti* in flowers (mean number of larvae and adults per flower), comparison among 5 seasons. Values are means ± SEM ((√p + 3/8) transformed), season effect; a) Larvae, n = 623, $F_{(4,10)} = 11.2$, $P < 0.01$; b) Adults, $F_{(4,10)} = 15.3$, $P < 0.01$.

a) LARVAE

Season / Region	I/95	II/95	I/96	II/96	I/97
Tokpa/Ayou	3.6 ± 0.3BD[1]	3.8 ± 0.2AD	2.1 ± 0.2E	3.6 ± 0.2ABC	3.0 ± 0.2BC

b) ADULTS

Season	I/95	II/95	I/96	II/96	I/97
Region					
Tokpa/Ayou	3.4 ± 0.3BC[1]	3.9 ± 0.3B	2.4 ± 0.2D	4.8 ± 0.2A	2.9 ± 0.2CD

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 3.6. Tokpa/Ayou, densities of larvae and adults of *M. sjostedti* in flowers (mean number of larvae and adults per flower counted the same day), comparison among 5 seasons. Values are means ± SEM (arcsine √p transformed), season effects; a) Larvae, n = 416, $F_{(4,10)} = 4.5$, $P < 0.05$; b) Adults, $F_{(4,10)} = 9.3$, $P < 0.01$.

a) LARVAE

Season	I/95	II/95	I/96	II/96	I/97
Region					
Tokpa/Ayou	0.038 ± 0.006AB[1]	0.047 ± 0.006A	0.023 ± 0.005B	0.056 ± 0.006A	0.039 ± 0.005AB

b) ADULTS

Season	I/95	II/95	I/96	II/96	I/97
Region					
Tokpa/Ayou	0.036 ± 0.005BC[1]	0.045 ± 0.005B	0.028 ± 0.005C	0.068 ± 0.005A	0.039 ± 0.004BC

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 3.7. Lema, numbers of larvae and adults of *M. sjostedti* in flowers (mean number of larvae and adults per flower), comparison among 5 seasons. Values are means ± SEM ((√p + 3/8) transformed), season effects; a) Larvae, n = 660, $F_{(4,10)} = 3.6$, $P < 0.05$; b) Adults, $F_{(4,10)} = 10.2$, $P < 0.01$.

a) LARVAE

Season	I/95	II/95	I/96	II/96	I/97
Region					
Lema	2.4 ± 0.3B[1]	2.5 ± 0.3B	3.5 ± 0.3A	3.2 ± 0.3AB	3.7 ± 0.3A

b) ADULTS

Season	I/95	II/95	I/96	II/96	I/97
Region					
Lema	1.8 ± 0.4C[1]	3.3 ± 0.4B	4.1 ± 0.3AB	5.1 ± 0.3A	3.7 ± 0.3B

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 3.8. Lema, densities of larvae and adults of *M. sjostedti* in flowers on NPK levels (without/ with NPK) over 5 seasons (mean number of larvae and adults per flower counted the same day), comparison among 5 seasons and 2 NPK levels (larvae). Values are means ± SEM (arcsine √p transformed); a) Larvae, season*NPK interaction, n = 463, $F_{(8,423)} = 2.6$, $P < 0.05$; b) Adults, season effect, $F_{(4,10)} = 13.0$, $P < 0.01$.

a) LARVAE

Season	I/95	II/95	I/96	II/96	I/97
NPK					
Without	0.033 ± 0.007a[1]A[2]	0.034 ± 0.006aA	0.030 ± 0.006aA	0.058 ± 0.007aA	0.042 ± 0.006aA
With	0.031 ± 0.007aBC	0.027 ± 0.006aC	0.030 ± 0.006aC	0.050 ± 0.006aAB	0.056 ± 0.006aA

b) ADULTS

Season	I/95	II/95	I/96	II/96	I/97
	0.026 ± 0.007C[2]	0.040 ± 0.006BC	0.039 ± 0.006BC	0.089 ± 0.007A	0.047 ± 0.006B

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 3.9. IITA, numbers of larvae and adults of *M. sjostedti* in flowers over 5 seasons (mean number of larvae and adults per flower). Values are means ± SEM ((√p + 3/8) transformed), season effect; a) Larvae, n = 455, $F_{(4,10)} = 11.9$, $P < 0.01$; b) Adults, $F_{(4,10)} = 18.4$, $P << 0.01$.

a) LARVAE

Season	I/95	II/95	I/96	II/96	I/97
Region					
IITA	4.1 ± 0.4A[1]	5.1 ± 0.3A	3.2 ± 0.3AB	3.2 ± 0.3AB	2.4 ± 0.3B

b) ADULTS

Season	I/95	II/95	I/96	II/96	I/97
Region					
IITA	4.2 ± 0.4AB[1]	5.0 ± 0.3A	3.4 ± 0.3B	2.4 ± 0.3C	2.3 ± 0.2C

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 3.10. IITA, densities of larvae and adults of *M. sjostedti* in flowers on 5 seasons (mean number of larvae and adults per flower counted the same day). Values are means ± SEM (arcsine √p transformed), season effect; a) Larvae, n = 287, $P \geq 0.05$; b) Adults, $F_{(4,10)} = 4.5$, $P < 0.05$.

a) LARVAE

Season / Region	I/95	II/95	I/96	II/96	I/97
IITA	0.043 ± 0.008A[1]	0.068 ± 0.006A	0.047 ± 0.007A	0.060 ± 0.008A	0.043 ± 0.008A

b) ADULTS

Season / Region	I/95	II/95	I/96	II/96	I/97
IITA	0.040 ± 0.006BC[1]	0.064 ± 0.005A	0.044 ± 0.006BC	0.040 ± 0.006B	0.036 ± 0.006C

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 4.1. Larval mortality of *M. vitrata* in flowers and pods due to parasitism, comparison among 5 seasons across 3 regions. Values are mean percentage ± SEM (detransformed from logit), $n_{t,e,l}$ = number of observations for total larvae (n_t), early instars (n_e, instars 1-3) and late instars (n_l, instars 4, 5), trials = number of larvae investigated for parasitism; a) Flowers: n_t = 740, trials = 10,855, c^2 = 166.0, df = 4, $P << 0.01$; n_e = 612, trials = 6,062, c^2 = 151.7, df = 4, $P << 0.01$; n_l = 619, trials = 4,793, c^2 = 83.5, df = 4, $P << 0.01$; b) Pods: n_t = 270, trials = 1,210, $P \geq 0.05$; n_l = 248, trials = 1,046, $P \geq 0.05$.

Season	I/95	II/95	I/96	II/96	I/97
a) FLOWERS					
Total larvae	14.0 ± 1.7A[1]	15.8 ± 1.5A	7.8 ± 0.4C	17.6 ± 0.7A	10.2 ± 0.5B
Early instars	15.5 ± 3.3BCD	18.0 ± 2.3B	11.6 ± 0.7C	25.7 ± 1.0A	13.8 ± 0.8D
Late instars	11.6 ± 1.8A	13.7 ± 1.9A	2.3 ± 0.4C	5.7 ± 0.7B	6.0 ± 0.6B
b) PODS					
Total larvae	8.3 ± 2.7A[1]	8.0 ± 7.6A	5.2 ± 1.1A	8.3 ± 1.9A	9.5 ± 2.1A
Late instars	9.6 ± 3.1A	12.1 ± 10.5A	3.6 ± 0.9A	4.3 ± 1.4A	9.4 ± 2.4A

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$. Instar groups (total, early, late) were not compared among each other.

Table 4.2. Larval mortality of *M. sjostedti* in flowers due to parasitism across three regions. Values are mean percentage ± SEM (detransformed from logit), n = observations used, trials = number of larvae investigated for parasitism; a) Comparison among seasons (across regions), n = 851, trials = 62,524, c^2 = 686.9, df = 4, $P << 0.01$; b) Comparison of mulch types *S. siamea* and *I. cylindrica* against the control among regions (interaction), c^2 = 15.9, df = 4, $P < 0.01$.

a) Season	I/95	II/95	I/96	II/96	I/97
Larvae	2.5 ± 0.36A[2]	0.1 ± 0.03D	1.6 ± 0.11B	0.4 ± 0.05C	3.2 ± 0.12A

b) Mulch Region	Control	*S. siamea*	*I. cylindrica*
IITA	0.2 ± 0.08c[1]A[2]	0.3 ± 0.07cA	0.4 ± 0.10cA
Lema	2.9 ± 0.18aA	3.1 ± 0.2aA	2.7 ± 0.18aA
Tokpa/Ayou	1.3 ± 0.12bA	0.8 ± 0.09bA	1.1 ± 0.11bA

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.

[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$. The interaction region*mulch was significant between Lema and Tokpa/Ayou on control versus *S. siamea* and *S. siamea* versus *I. cylindrica.*

Table 4.3. Larval mortality of *M. vitrata* (all instars together) in flowers due to parasitism, comparison among 2 regions (Lema, Tokpa/Ayou) with 2 NPK levels (without/ with NPK) and 2 mulch types, *S. siamea* and *I. cylindrica*, against a control. Values are mean percentage ± SEM (detransformed from logit), n = observations used, trials = number of larvae investigated for parasitism region*NPK*mulch interaction, n = 622, trials = 9,146, c^2 = 6.3, df = 2, $P < 0.05$.

Mulch Total larvae Region	NPK	Control	*S. siamea*	*I. cylindrica*
Lema	**without**	18.1 ± 1.35b[1]A[2]	15.2 ± 1.14bB	17.1 ± 1.35bA
	with	23.4 ± 1.16aA	18.9 ± 1.31aA	21.0 ± 1.39aA
Tokpa/Ayou	**without**	4.5 ± 0.89cA	2.0 ± 0.59cB	3.8 ± 0.83cA
	with	4.3 ± 0.86cA	5.4 ± 1.09cA	3.5 ± 0.73cA

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 4.4. Larval mortality of *M. vitrata* in pods due to parasitism, comparison among 2 NPK levels (without/ with NPK) and 2 mulch types, *S. siamea* and *I. cylindrica*, against a control across regions Lema and Tokpa/Ayou. Values are mean percentage ± SEM (detransformed from logit) for total larvae (all instars), early instars (instars 1, 2, 3) and late instars (instars 4, 5), effects of NPK and mulch, n = observations used, trials = number of larvae investigated for parasitism; a) Total larvae (all instars), NPK*mulch interaction, n = 209, trials = 925, c^2 = 9.1, df = 2, $P < 0.05$; b) Early instars, NPK*mulch interaction, n = 79, trials = 135, c^2 = 7.1, df = 2, $P < 0.05$; c) Late instars, NPK*mulch interaction, n = 191, trials = 790, c^2 = 6.3, df = 2, $P < 0.05$.

a) Total larvae

Mulch NPK	Control	*S. siamea*	*I. cylindrica*
Without	14.0 ± 3.5a[1]A[2]	7.2 ± 3.2aB	4.8 ± 2.4aB
With	5.6 ± 1.7aB	11.6 ± 2.9aA	7.8 ± 2.1aAB

b) Early instars

Mulch NPK	Control	*S. siamea*	*I. cylindrica*
Without	32.0 ± 11.1a[1]A[2]	0.0 ± 0.0aB	0.0 ± 0.0aB
With	20.0 ± 6.4aA	34.2 ± 8.2aA	9.6 ± 5.1aA

No NPK effect occurred across mulch treatments.

c) Late instars

Mulch / NPK	Control	*S. siamea*	*I. cylindrica*
Without	10.6 ± 3.1a[1]A[2]	7.0 ± 3.1aA	5.8 ± 2.8aA
With	3.2 ± 1.2aB	8.5 ± 2.3aA	8.5 ± 2.0aA

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 4.5. Larval mortality of *M. sjostedti* in flowers due to parasitism, comparison among 2 NPK levels (without/ with NPK) and 2 mulch types, *S. siamea* and *I. cylindrica*, against a control across regions Lema and Tokpa/Ayou. Values are mean percentage ± SEM (detransformed from logit), n = observations used, trials = number of larvae investigated for parasitism; NPK main effect, n = 686, trials = 50,788, $c^2 = 83.5$, df = 1, $P << 0.01$.

Mulch / NPK	Control	*S. siamea*	*I. cylindrica*
Without	1.5 ± 0.13a[1]A[2]	1.3 ± 0.12aA	1.2 ± 0.11aA
With	2.7 ± 0.17bA	2.9 ± 0.21bA	2.7 ± 0.18bA

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 4.6. Larval mortality of *M. vitrata* in flowers due to parasitism, comparison among 5 seasons and on a NPK*mulch effect across seasons in Tokpa/Ayou. Values are mean percentage ± SEM (detransformed from logit), $n_{t,e,l}$ = number of observations for total larvae (n_t), early instars (n_e, instars 1-3) and late instars (n_l, instars 4, 5), trials = number of larvae investigated for parasitism; a) Effect on seasons: $n_t = 311$, trials = 3,588, $c^2 = 90.8$, df = 4, $P << 0.01$; $n_e = 256$, trials = 1,679, $c^2 = 53.4$, df = 4, $P << 0.01$; $n_l = 249$, trials = 1,909, $c^2 = 57.3$, df = 4, $P << 0.01$; b) NPK*mulch interaction, on 2 NPK levels (without/ with NPK) and 2 mulch types, *S. siamea* and *I. cylindrica*, against a control: late instars, $n_l = 249$, trials = 1,909, $c^2 = 8.7$, df = 2, $P < 0.05$.

a) Seasonal effects

Season	I/95	II/95	I/96	II/96	I/97
Total larvae	7.6 ± 1.5B[1]	6.9 ± 2.2AB	0.4 ± 0.2D	12.4 ± 2.6A	3.2 ± 0.4C
Early instars	5.2 ± 2.2B	4.2 ± 2.8BC	0.4 ± 0.2C	11.1 ± 3.1A	5.3 ± 0.8B
Late instars	9.0 ± 2.0A	8.9 ± 3.3A	0.4 ± 0.3B	11.9 ± 3.7A	1.7 ± 0.4B

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.
Instar groups (total, early, late) were not compared among each other.

b) NPK*mulch interaction

Mulch	Control	*S. siamea*	*I. cylindrica*
NPK			
Without	2.7 ± 0.9a[1]A[2]	0.8 ± 0.5bA	3.1 ± 0.9aA
With	2.9 ± 1.0aA	5.0 ± 1.2aA	2.4 ± 0.8aA

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 4.7. Larval mortality of *M. sjostedti* in flowers due to parasitism, comparison among 5 seasons on 2 NPK levels (without/ with NPK) and 2 mulch types, *S. siamea* and *I. cylindrica*, against a control in Tokpa/Ayou. season II/95 was discarded from analysis. Values are mean percentage ± SEM (detransformed from logit), n = observations used, trials = number of larvae investigated for parasitism; season main effect, n = 292, trials = 22,222, c^2 = 119.3, df = 3, $P << 0.01$; season*NPK*mulch interaction, c^2 = 18.9, df = 6, $P < 0.01$.

Season	Mulch NPK	Control	*S. siamea*	*I. cylindrica*
I/95	**without**	1.9 ± 0.9	2.3 ± 0.8	2.6 ± 0.9
	with	3.4 ± 1.1	1.4 ± 0.6	2.1 ± 0.8
II/95	**without**	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1
	with	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
I/96	**without**	2.4 ± 0.6	2.3 ± 0.6	1.4 ± 0.4
	with	4.1 ± 0.6	1.5 ± 0.4	5.0 ± 0.8
II/96	**without**	0.1 ± 0.1	0.1 ± 0.1	0.4 ± 0.2
	with	0.9 ± 0.3	0.2 ± 0.1	0.6 ± 0.2
I/97	**without**	1.1 ± 0.3	0.4 ± 0.0	0.7 ± 0.2
	with	1.6 ± 0.3	1.4 ± 0.0	0.8 ± 0.2

Means were not marked with letters since no attempt was made to formulate the mutual comparisons.

Table 4.8. Larval mortality of *M. vitrata* (early instars) in flowers due to parasitism, comparison on a season*NPK*mulch interaction for 4 seasons with 2 NPK levels (without/ with NPK) and 2 mulch types, *S. siamea* and *I. cylindrica*, against a control in Lema. Season I/95 was discarded due to few larvae only. Values are mean percentage ± SEM (detransformed from logit) on total larvae, n = number of observations, trials = number of larvae investigated for parasitism; NPK main effect, n = 277, trials = 5,417, c^2 = 25.0, df = 1, $P << 0.01$; season*NPK*mulch interaction, c^2 = 21.8, df = 8, $P < 0.01$.

Early instars	Mulch	Control	*S. siamea*	*I. cylindrica*
Season	**NPK**			
II/95	**Without**	8.1 ± 4.5	14.6 ± 5.1	23.9 ± 6.3
	With	35.8 ± 5.9	34.0 ± 6.5	25.4 ± 5.7
I/96	**Without**	19.1 ± 2.4	10.2 ± 1.9	8.7 ± 1.6
	With	19.6 ± 2.2	11.8 ± 1.6	18.9 ± 2.3
II/96	**Without**	28.7 ± 3.3	19.9 ± 2.9	19.8 ± 3.0
	With	37.9 ± 2.2	24.3 ± 2.5	29.5 ± 2.5
I/97	**Without**	10.3 ± 1.8	17.1 ± 1.8	25.8 ± 3.0
	With	13.8 ± 1.9	24.1 ± 3.4	18.0 ± 3.1

Means were not marked with letters since no attempt was made to fully formulate the mutual comparisons.

Table 4.9. Larval mortality of *M. vitrata* (late instars) in flowers due to parasitism, comparison among 5 seasons and 2 mulch treatments, *S. siamea* and *I. cylindrica*, against a control in Lema. Values are mean percentage ± SEM (detransformed from logit), n = number of observations, trials = number of larvae investigated for parasitism; season main effect, n = 271, trials = 1,962, c^2 = 37.4, df = 4, $P << 0.01$; season*mulch interaction, c^2 = 23.9, df = 8, $P < 0.01$.

Mulch	Control	*S. siamea*	*I. cylindrica*
Season			
I/95	25.1 ± 6.4	15.4 ± 9.2	4.6 ± 4.4
II/95	12.4 ± 5.3	30.2 ± 5.9	22.9 ± 5.4
I/96	6.1 ± 1.8	3.8 ± 1.3	5.2 ± 1.5
II/96	8.2 ± 2.0	15.0 ± 3.0	6.1 ± 1.7
I/97	8.3 ± 1.9	14.7 ± 2.7	17.4 ± 3.1

Means were not marked with letters since no attempt was made to fully formulate the mutual comparisons.

Table 4.10. Larval mortality of *M. sjostedti* in flowers due to parasitism, comparison among 3 seasons on 2 NPK levels (without/ with NPK) and 2 mulch types, *S. siamea* and *I. cylindrica*, against a control in Lema. Seasons I/95 and II/95 were discarded from analysis due to no or too few parasitism events. Values are mean percentage ± SEM (detransformed from logit), n = observations used, trials = number of larvae investigated for parasitism; NPK main effect, n = 247, trials = 20,950, c^2 = 78.9, df = 1, $P << 0.01$; season main effect, c^2 = 684.2, df = 2, $P << 0.01$; season*NPK*mulch interaction, c^2 = 13.2, df = 6, $P < 0.05$.

Mulch		Control	*S. siamea*	*I. cylindrica*
Season	**NPK**			
I/96	**without**	1.1 ± 0.4	0.7 ± 0.3	0.0 ± 0.0
	with	1.8 ± 0.4	2.5 ± 0.5	1.3 ± 0.4
II/96	**without**	0.0 ± 0.0	0.3 ± 0.2	0.1 ± 0.1
	with	0.4 ± 0.2	2.2 ± 0.4	1.2 ± 0.3
I/97	**without**	5.2 ± 0.5	4.9 ± 0.5	5.3 ± 0.6
	with	9.4 ± 0.8	12.1 ± 1.2	10.2 ± 1.0

Means were not marked with letters since no attempt was made to fully formulate the mutual comparisons.

Table 4.11. Mortality of eggs of *M. vitrata* exposed on carrier plants due to parasitism, comparison among 4 seasons and 3 mulch treatments, *S. siamea*, *I. cylindrica* and *A. indica* against a control at IITA. Values are mean percentage ± SEM (detransformed from logit), n = number of observations, trials = number of larvae investigated for parasitism; season main effect, n = 244, trials = 5,038, c^2 = 111.7, df = 3, $P << 0.01$; mulch main effect, c^2 = 19.8, df = 3, $P < 0.01$; season*mulch interaction, c^2 = 35.9, df = 9, $P << 0.01$.

Mulch	Control	*S. siamea*	*I. cylindrica*	*A. indica*
Season				
II/95	26.0 ± 3.4AB[1]	18.1 ± 3.8A	11.3 ± 2.7B	16.2 ± 3.1AB
I/96	19.4 ± 2.0AB	16.8 ± 1.9A	10.7 ± 1.5B	25.1 ± 2.3AB
II/96	2.1 ± 1.1AB	3.9 ± 1.4A	3.1 ± 1.1B	6.0 ± 1.8AB
I/97	10.3 ± 1.3AB	21.3 ± 1.8A	9.3 ± 1.3B	15.8 ± 1.6AB

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.
The season main effect applied generally except for *S. siamea* mulch in season I/97, this value was relatively elevated and was not smaller than *S. siamea* in seasons II/95 and I/96 as suggested by the overall results across mulch.

Table 4.12. Larval mortality of *M. sjostedti* in flowers due to parasitism, comparison among 3 seasons and 3 mulch types, *S. siamea*, *I. cylindrica* and *A. indica* against a control at IITA. Seasons II/95 and II/96 were discarded from analysis due to no or too few parasitism events. Values are mean percentage ± SEM (detransformed from logit), n = observations used, trials = number of larvae investigated for parasitism; season main effect, n = 139, trials = 9,946, c^2 = 11.0, df = 2, $P < 0.01$; season*mulch interaction, c^2 = 13.8, df = 6, $P < 0.05$.

Mulch	**Control**	***S. siamea***	***I. cylindrica***	***A. indica***
Season				
I/95	0.9 ± 0.5	0.3 ± 0.3	0.6 ± 0.5	0.0 ± 0.0
I/96	0.3 ± 0.2	0.5 ± 0.2	0.9 ± 0.3	1.2 ± 0.3
I/97	0.2 ± 0.1	0.4 ± 0.2	0.1 ± 0.1	0.1 ± 0.1

Table 4.13. Tokpa/Ayou, season I/95, larval mortality of *M. vitrata* and *M. sjostedti* in flowers due to parasitism, comparison among 2 NPK levels (without/ with NPK) on 2 sampling days (DAP 56, 63). Values are mean percentage ± SEM (detransformed from logit), (n) = number of larvae on which mortality is based, n = observations used, trials = number of larvae investigated for parasitism; a) *M. vitrata*, total larvae, trend on NPK profiles, n = 32, trials = 232, c^2 = 4.3, df = 1, $P < 0.05$; b) *M. sjostedti*, trend on NPK profiles, n = 33, trials = 1,459, c^2 = 13.9, df = 1, $P < 0.01$.

a) *M. vitrata*

DAP	**56**	**63**
NPK		
Without	2.6 ± 2.5	5.7 ± 2.3
(n)	(47)	(86)
With	19.1 ± 5.9	4.6 ± 2.6
(n)	(42)	(57)

b) *M. sjostedti*

DAP	**56**	**63**
NPK		
Without	2.8 ± 1.0	2.9 ± 0.8
(n)	(257)	(440)
With	6.5 ± 1.5	0.4 ± 0.3
(n)	(303)	(459)

No main effects were found but the interaction NPK*DAP was significant for larvae of *M. vitrata* and *M. sjostedti* in flowers at $P < 0.05$.

Table 4.14. Tokpa/Ayou, season I/96, larval mortality of *M. sjostedti* in flowers due to parasitism, comparison among 2 NPK levels (without/ with NPK) and 2 mulch types, *S. siamea* and *I. cylindrica* against a control on 4 sampling days (DAP 49-70). Values are mean percentage ± SEM (detransformed from logit), (n) = number of larvae on which mortality is based, n = observations used, trials = number of larvae investigated for parasitism; a) NPK*mulch interaction, n = 65, trials = 4,541, c^2 = 11.1, df = 2, $P < 0.01$; b) Time (DAP) main effect, c^2 = 13.7, df = 3, $P < 0.01$.

a) Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	2.3 ± 0.5	2.2 ± 0.5	1.4 ± 0.4
(n)	(718)	(672)	(674)
With	4.1 ± 0.7	1.6 ± 0.4	5.0 ± 0.8
(n)	(804)	(881)	(792)

No main effects were found.

b) DAP	**49**	**56**	**63**	**70**
	4.4 ± 0.7A[1]	2.9 ± 0.4B	2.6 ± 0.4B	1.0 ± 0.6C
(n)	(614)	(1,628)	(1,939)	(360)

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 4.15. Tokpa/Ayou, season II/96, relative dominance of the three parasitoids *Dolichogenidea* sp., *Phanerotoma leucobasis* and *Braunsia kriegeri* ovipositing in larvae of *M. vitrata* in flowers, comparison among 2 sampling days (DAP 56, 63). Values are mean percentage ± SEM (detransformed from logit), (n) = number of parasitized larvae per DAP, n = observations used, trials = number of larvae investigated for parasitism; interaction of parasitoid with time (DAP), n = 96, trials = 125, c^2 = 9.7, df = 2, $P < 0.01$.

DAP	**56**	**63**
(n)	(3)	(13)
***Dolichogenidea* sp.**	66.7 ± 27.2	0.0 ± 0.0
P. leucobasis	33.3 ± 27.2	46.7 ± 12.9
B. kriegeri	0.0 ± 0.0	40.0 ± 12.6

At DAP 63 one larva was parasitized by *Pristomerus* sp., which was not included in the analysis. No main effects occurred, but parasitoids interacted with DAP.

Table 4.16. Tokpa/Ayou, season I/97, larval mortality of *M. vitrata* in flowers due to parasitism, comparison among 2 mulch types, *S. siamea* and *I. cylindrica* against a control on 3 sampling days (DAP 49-63). Values are mean percentage ± SEM (detransformed from logit), (n) = number of larvae on which mortality is based, n = observations used, trials = number of larvae investigated for parasitism; mulch main effect, n = 54, trials = 1,817, c^2 = 19.7, df = 2, $P < 0.01$; time main effect, c^2 = 10.3, df = 2, $P < 0.01$.

DAP	**49**	**56**	**63**
Mulch			
Control	6.3 ± 2.1	5.1 ± 1.1	4.7 ± 1.9
(n)	(131)	(394)	(128)
S. siamea	0.0 ± 0.0	3.1 ± 1.0	0.0 ± 0.0
(n)	(87)	(320)	(131)
I. cylindrica	3.1 ± 2.2	3.4 ± 0.9	1.3 ± 0.9
(n)	(85)	(570)	(160)

Table 4.17. Tokpa/Ayou, season I/97, relative dominance of the two parasitoids, *Phanerotoma leucobasis* and *Braunsia kriegeri* ovipositing in larvae of *M. vitrata* in flowers, comparison among 3 sampling days (DAP 49-63). Values are mean percentage ± SEM (detransformed from logit), (n) = number of parasitized larvae per DAP, n = observations used, trials = number of larvae investigated for parasitism; interaction of parasitoid with time (DAP), n = 108, trials = 3,634, c^2 = 14.1, df = 2, $P < 0.01$.

DAP	**49**	**56**	**63**
Mulch			
(n)	(10)	(42)	(8)
P. leucobasis	90.0 ± 9.5	76.2 ± 6.6	25.0 ± 15.3
B. kriegeri	0.0 ± 0.0	23.8 ± 6.6	75.0 ± 15.3

The interaction between parasitoid species and time (DAP) was significant at $P \geq 0.05$. At DAP 49 one larva of *Dolichogenidea* sp. was found in addition.

Table 4.18. Tokpa/Ayou, season I/97, larval mortality of *M. vitrata* in pods due to parasitism, comparison among 2 NPK levels (without/ with NPK) and 2 mulch types, *S. siamea* and *I. cylindrica* against a control on 3 sampling days (DAP 56-70). Values are mean percentage ± SEM (detransformed from logit), (n) = number of larvae on which mortality is based, n = observations used, trials = number of larvae investigated for parasitism; NPK*mulch interaction, n = 47, trials = 348, c^2 = 7.3, df = 2, $P < 0.05$.

Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	11.9 ± 3.9	0.0 ± 0.0	2.6 ± 2.6
(n)	(65)	(24)	(32)
With	2.6 ± 1.5	4.8 ± 2.3	2.9 ± 2.0
(n)	(103)	(59)	(65)

No main effects were found.

Table 4.19. Tokpa/Ayou, season I/97, larval mortality of *M. sjostedti* in flowers due to parasitism, comparison among 2 NPK levels (without/ with NPK) and 2 mulch types, *S. siamea* and *I. cylindrica* against a control on 4 sampling days (DAP 49-70). Values are mean percentage ± SEM (detransformed from logit), (n) = number of larvae on which mortality is based, n = observations used, trials = number of larvae investigated for parasitism; NPK main effect, n = 72, trials = 8,029, c^2 = 7.6, df = 1, $P < 0.01$; NPK*mulch interaction, c^2 = 9.8, df = 2, $P < 0.01$.

Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	1.1 ± 0.3	0.4 ± 0.2	0.8 ± 0.2
(n)	(1,361)	(1,443)	(1,476)
With	1.4 ± 0.3	1.8 ± 0.4	0.9 ± 0.3
(n)	(1,403)	(1,128)	(1,218)

Table 4.20. Lema, season I/95, larval mortality of *M. vitrata* in flowers due to parasitism, comparison among 2 NPK levels (without/ with NPK) and 2 mulch types, *S. siamea* and *I. cylindrica* against a control on DAP 49. Values are mean percentage ± SEM (detransformed from logit), (n) = number of larvae on which mortality is based, n = observations used, trials = number of larvae investigated for parasitism; NPK*mulch interaction, n = 46, trials = 114, c^2 = 12.1, df = 2, $P < 0.01$.

Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	34.8 ± 9.9	0.0 ± 0.0	7.1 ± 6.9
(n)	(23)	(21)	(14)
With	25.0 ± 7.2	38.5 ± 13.5	0.0 ± 0.0
(n)	(36)	(13)	(7)

Table 4.21. Lema, season II/95, larval mortality of *M. vitrata* in flowers due to parasitism, comparison among 2 NPK levels (without/ with NPK) and 2 mulch types, *S. siamea* and *I. cylindrica* against a control on 2 sampling days (DAP 49, 56). Values are mean percentage ± SEM (detransformed from logit), (n) = number of larvae on which mortality is based, n = observations used, trials = number of larvae investigated for parasitism; a) Total larvae, NPK*mulch interaction, n = 33, trials = 295, c^2 = 7.8, df = 2, $P < 0.05$; b) Early instars, NPK main effect, n = 30, trials = 145, c^2 = 7.3, df = 1, $P < 0.01$; NPK*mulch interaction, c^2 = 7.4, df = 2, $P < 0.05$; c) Late instars, n = 31, trials = 150, $P \geq 0.05$.

a) Total larvae[1]

Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	8.7 ± 4.7	15.2 ± 5.3	28.8 ± 7.0
(n)	(35)	(46)	(42)
With	35.8 ± 5.9	35.3 ± 6.7	25.1 ± 5.8
(n)	(65)	(52)	(55)

b) Early instars[2]

Without	4.9 ± 4.7	16.8 ± 7.6	29.4 ± 10.7
(n)	(20)	(24)	(17)
With	51.6 ± 7.9	22.1 ± 8.6	36.4 ± 10.5
(n)	(40)	(24)	(20)

c) Late instars[1]

Without	13.6 ± 9.0	13.6 ± 7.3	27.2 ± 8.9
(n)	(15)	(22)	(25)
With	11.8 ± 6.4	46.7 ± 9.5	20.5 ± 7.1
(n)	(25)	(28)	(35)

[1] No main effects were found.
[2] The NPK main effect was significant at $P < 0.05$.

Table 4.22. Lema, season II/95, relative dominance of three parasitoids, *Dolichogenidea* sp., *Phanerotoma leucobasis* and *Braunsia kriegeri* ovipositing in larvae of *M. vitrata* in flowers on 2 sampling days (DAP 49, 56). Values are mean percentage ± SEM (detransformed from logit), (n) = number of parasitized larvae per mulch treatment or per DAP, n = observations used, trials = number of larvae investigated for parasitism; a) Parasitoids in 2 mulch types, *S. siamea* and *I. cylindrica* against a control, n = 99, trials = 295, $c^2 = 26.7$, df = 4, $P << 0.01$; b) Parasitoids between time points DAP 49, 56, $c^2 = 8.6$, df = 2, $P < 0.05$.

a) Mulch	**Control**	***S. siamea***	***I. cylindrica***	**b) DAP**	**49**	**56**
Parasitoid						
(n)	(27)	(25)	(25)		(67)	(10)
Dolichogenidea sp.	7.0 ± 4.7	0.0 ± 0.0	0.0 ± 0.0		2.8 ± 1.9	0.0 ± 0.0
P. leucobasis	71.2 ± 8.2	20.6 ± 8.1	41.1 ± 9.6		49.8 ± 5.5	13.2 ± 11.5
B. kriegeri	21.5 ± 7.4	79.4 ± 8.1	58.8 ± 9.6		47.4 ± 5.3	85.8 ± 11.9

No main effects were found. Slight departures from 100% across the 3 parasitoids in columns for the control and *Imperata* are due to rounding errors.

Table 4.23. Lema, season I/96, larval mortality of *M. vitrata* (total larvae) in flowers due to parasitism on 3 sampling days (DAP 42-56), comparison of 2 mulch types, *S. siamea* and *I. cylindrica* against a control interacting with 2 NPK levels (without/ with NPK) and time (DAP) respectively. Values are mean percentage ± SEM (detransformed from logit), (n) = number of larvae on which mortality is based, n = observations used, trials = number of larvae investigated for parasitism; a) NPK main effect, n = 50, trials = 1,694, $c^2 = 10.7$, df = 1, $P < 0.01$; NPK*mulch interaction, $c^2 = 8.2$, df = 2, $P < 0.05$; b) Trend on mulch profiles, $P \geq 0.05$.

a) Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	18.2 ± 2.3A[1]	10.7 ± 2.0B	8.9 ± 1.6B
(n)	(274)	(244)	(292)
With	23.1 ± 2.6A	12.7 ± 1.8B	22.4 ± 2.7A
(n)	(279)	(357)	(248)

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

b) DAP	42	49	56
Mulch			
Control	16.2 ± 4.6	23.9 ± 2.3	14.4 ± 3.1
(n)	(58)	(368)	(127)
S. siamea	10.7 ± 5.0	10.6 ± 1.6	15.0 ± 2.8
(n)	(38)	(395)	(168)
I. cylindrica	11.4 ± 2.6	15.4 ± 2.0	18.6 ± 3.3
(n)	(50)	(341)	(149)

Table 4.24. Lema, season I/96, relative dominance of three parasitoids, *Dolichogenidea* sp., *Phanerotoma leucobasis* and *Braunsia kriegeri* ovipositing in larvae of *M. vitrata* in flowers on 3 sampling days (DAP 42-56). Values are mean percentage ± SEM (detransformed from logit), (n) = number of parasitized larvae per DAP, n = observations used, trials = number of larvae investigated for parasitism; main effect among parasitoids, n = 150, trials = 1,694, c^2 = 147.2, df = 2, $P << 0.01$; trend of parasitoids' profiles over time (DAP), $c^2 = 19.0^{[q]}$, df = 4, $P < 0.01$.

DAP	42	49	56
Parasitoid			
(n)	(22)	(178)	(69)
Dolichogenidea sp.	4.6 ± 4.5	3.5 ± 1.4	3.9 ± 2.2
P. leucobasis	82.2 ± 8.2	89.7 ± 2.3	68.9 ± 5.7
B. kriegeri	13.2 ± 7.2	6.8 ± 1.9	27.6 ± 5.6

The time main effect (DAP) was not significantly different at $P \geq 0.05$.

Table 4.25. Lema, season I/96, larval mortality of *M. sjostedti* in flowers due to parasitism on 5 sampling days (DAP 42-70), comparison of 2 NPK levels (without/ with NPK) and 2 mulch types, *S. siamea* and *I. cylindrica* against a control. Values are mean percentage ± SEM (detransformed from logit), (n) = number of larvae on which mortality is based, n = observations used, trials = number of larvae investigated for parasitism; NPK main effect, n = 71, trials = 4,633, c^2 = 7.1, df = 1, $P < 0.01$; NPK*mulch interaction, c^2 = 10.9, df = 2, $P < 0.01$.

Mulch	Control	*S. siamea*	*I. cylindrica*
NPK			
Without	1.1 ± 0.5A[1]	0.5 ± 0.2A	0.0 ± 0.0A
(n)	(668)	(820)	(730)
With	2.2 ± 0.5A	2.3 ± 0.5A	1.1 ± 0.3B
(n)	(1017)	(826)	(961)

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 4.26. Lema, season II/96, larval mortality of *M. vitrata* in flowers due to parasitism on 2 sampling days (DAP 49, 56), comparison of 5 instars on 2 mulch types, *S. siamea* and *I. cylindrica* against a control. Values are mean percentage ± SEM (detransformed from logit), (n) = number of larvae on which mortality is based, n = observations used, trials = number of larvae investigated for parasitism; larval main effect, n = 155, trials = 1,479, c^2 = 144.3, df = 4, $P << 0.01$; instar*mulch interaction, c^2 = 31.7, df = 8, $P << 0.01$.

Mulch	**Control**	***S. siamea***	***I. cylindrica***
Instar			
1st instar	42.5 ± 4.5	41.7 ± 6.0	43.1 ± 5.7
(n)	(129)	(65)	(71)
2nd instar	62.5 ± 3.9	31.2 ± 4.6	49.0 ± 4.7
(n)	(159)	(97)	(110)
3rd instar	36.1 ± 3.7	16.7 ± 3.1	36.2 ± 4.6
(n)	(162)	(137)	(103)
4th instar	23.8 ± 6.4	29.4 ± 6.9	13.2 ± 4.3
(n)	(47)	(52)	(73)
5th instar	5.9 ± 2.4	11.9 ± 3.8	4.2 ± 2.1
(n)	(97)	(76)	(101)

The general larval main effect did not apply for *Senna* when comparing 4th with 5th instars.

Table 4.27. Lema, season II/96, larval mortality of *M. vitrata* in flowers due to parasitism on 2 sampling days (DAP 49, 56), comparison of 2 NPK levels (without/ with NPK) and 2 mulch types, *S. siamea* and *I. cylindrica* against a control. Values are mean percentage ± SEM (detransformed from logit), (n) = number of larvae on which mortality is based, n = observations used, trials = number of larvae investigated for parasitism; a) Total larvae, NPK main effect, n = 36, trials = 1,479, c^2 = 31.9, df = 1, $P << 0.01$; mulch main effect, c^2 = 25.4, df = 2, $P << 0.01$; b) Early instars, NPK main effect, n = 34, trials = 1,033, c^2 = 21.9, df = 1, $P << 0.01$; mulch main effect, c^2 = 34.6, df = 2, $P << 0.01$; c) Late instars, mulch main effect, n = 34, trials = 446, c^2 = 7.0, df = 2, $P < 0.05$.

	Mulch	**Control**	***S. siamea***	***I. cylindrica***
a)	**Total larvae**			
	NPK			
	Without	28.2 ± 3.3b[1]A[2]	20.3 ± 3.0bA	20.2 ± 3.0bA
	(n)	(185)	(183)	(181)
	With	45.5 ± 2.4aA	27.5 ± 2.8aC	37.2 ± 2.9aB
	(n)	(409)	(244)	(277)

b) Early instars

Without	40.8 ± 4.6b[1]A[2]	20.8 ± 3.8bB	29.2 ± 4.4bB
(n)	(113)	(115)	(106)
With	53.0 ± 2.7aA	32.0 ± 3.5aB	52.5 ± 3.7aA
(n)	(337)	(184)	(178)

c) Late instars

Without	9.1 ± 3.3a[1]A[23]	19.4 ± 4.8aA	6.8 ± 2.9aA
(n)	(72)	(68)	(75)
With	12.3 ± 3.8aA	14.5 ± 4.5aA	7.7 ± 2.8aA
(n)	(72)	(60)	(99)

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.
[3] Simple effects (without/ with NPK) were not significantly different but overall mulch main effects displayed significant variation between *Senna* and *Imperata*.

Table 4.28. Lema, season II/96, relative dominance of three parasitoids, *Dolichogenidea* sp., *Phanerotoma leucobasis* and *Braunsia kriegeri* ovipositing in larvae of *M. vitrata* in flowers on 2 sampling days (DAP 49, 56). Values are mean percentage ± SEM (detransformed from logit), (n) = number of parasitized larvae per DAP, n = observations used, trials = number of larvae investigated for parasitism; main effect among parasitoids, n = 108, trials = 1,479, $c^2 = 172.1$, df = 2, $P << 0.01$; parasitoids on NPK levels, $c^2 = 19.2$, df = 2, $P << 0.01$.

NPK	**without**	**with**
Parasitoid		
(n)	(22)	(178)
Dolichogenidea sp.	19.8 ± 3.6b[1]	27.8 ± 2.4b
P. leucobasis	61.0 ± 4.3a	65.2 ± 2.5a
B. kriegeri	18.1 ± 3.4b	5.8 ± 1.3c

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.

Table 4.29. Lema, season II/96, larval mortality of *M. sjostedti* in flowers due to parasitism on 2 sampling days (DAP 49, 56), comparison of 2 NPK levels (without/ with NPK) and 2 mulch types, *S. siamea* and *I. cylindrica* against a control. Values are mean percentage ± SEM (detransformed from logit), (n) = number of larvae on which mortality is based, n = observations used, trials = number of larvae investigated for parasitism; NPK main effect, n = 34, trials = 5,496, c^2 = 30.5, df = 1, $P << 0.01$; mulch main effect, c^2 = 28.5, df = 2, $P << 0.01$.

Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	0.0 ± 0.0b[1]A[2][3]	0.4 ± 0.2bA	0.1 ± 0.1bA
(n)	(816)	(868)	(978)
With	0.2 ± 0.1aC	2.5 ± 0.5aA	1.5 ± 0.4aB
(n)	(1,005)	(902)	(927)

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.
[3] Simple effects within non-fertilized plots were not significantly different but overall mulch main effects displayed significant variation at $P << 0.01$.

Table 4.30. Lema, season I/97, larval mortality of *M. vitrata* in flowers due to parasitism on 5 sampling days (DAP 42-70), comparison of 5 larval instars. Values are mean percentage ± SEM (detransformed from logit), (n) = number of larvae on which mortality is based, n = observations used, trials = number of larvae investigated for parasitism; larval mortality over time (DAP), n = 239, trials = 1,361, c^2 = 83.2, df = 12, $P << 0.01$.

DAP	**42**	**49**	**56**	**63**	**70**
Instar					
1st instar	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
(n)	(15)	(50)	(4)	(27)	(77)
2nd instar	21.7 ± 6.9	46.1 ± 3.7	0.0 ± 0.0	0.0 ± 0.0	3.5 ± 1.7
(n)	(36)	(183)	(10)	(44)	(116)
3rd instar	20.7 ± 5.5	38.1 ± 3.2	6.7 ± 6.4	3.0 ± 3.0	2.4 ± 1.7
(n)	(51)	(230)	(15)	(38)	(93)
4th instar	13.0 ± 5.0	17.7 ± 4.1	4.1 ± 4.0	0.0 ± 0.0	15.5 ± 6.0
(n)	(40)	(88)	(22)	(18)	(48)
5th instar	0.0 ± 0.0	11.1 ± 2.6	0.0 ± 0.0	13.8 ± 4.5	22.6 ± 5.4
(n)	(21)	(139)	(36)	(60)	(73)

Table 4.31. Lema, season I/97, larval mortality of *M. vitrata* in flowers due to parasitism, comparison of 2 NPK levels (without/ with NPK) and 2 mulch types, *S. siamea* and *I. cylindrica* against a control on 5 sampling days (DAP 42-70). Values are mean percentage ± SEM (detransformed from logit), (n) = number of larvae on which mortality is based, n = observations used, trials = number of larvae investigated for parasitism; a) NPK*mulch interaction, n = 76, trials = 1,534, c^2 = 10.6, df = 2, $P < 0.01$; b) Trend on NPK profiles, c^2 = 13.2, df = 4, $P < 0.05$.

a) Mulch / NPK	Control	*S. siamea*	*I. cylindrica*
Without	12.5 ± 2.1a[1]B[2]	17.1 ± 1.7aB	24.3 ± 2.6aA
(n)	(252)	(432)	(204)
With	16.6 ± 2.2aA	23.7 ± 3.8aA	15.5 ± 3.7aA
(n)	(338)	(158)	(150)

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

b) DAP / NPK	42	49	56	63	70
Without	10.2 ± 3.3	31.9 ± 2.4	1.7 ± 1.6	2.7 ± 1.5	4.3 ± 1.3
(n)	(76)	(409)	(53)	(95)	(255)
With	21.0 ± 4.8	26.1 ± 2.7	2.4 ± 2.3	8.3 ± 3.6	14.9 ± 5.3
(n)	(87)	(281)	(34)	(92)	(152)

Table 4.32. Lema, season I/97, relative dominance of three parasitoids, *Dolichogenidea* sp., *Phanerotoma leucobasis* and *Braunsia kriegeri* ovipositing in larvae of *M. vitrata* in flowers on 4 sampling days (DAP 42, 49, 63, 70). Values are mean percentage ± SEM (detransformed from logit), (n) = number of parasitized larvae per DAP, n = observations used, trials = number of larvae investigated for parasitism; trend of parasitoids' profiles over time (DAP), n = 183, trials = 1,447, c^2 = 59.3, df = 6, $P << 0.01$.

DAP / Parasitoid	42	49	63	70
(n)	(27)	(206)	(9)	(26)
***Dolichogenidea* sp.**	4.5 ± 4.4	1.5 ± 0.9	0.0 ± 0.0	0.0 ± 0.0
P. leucobasis	75.8 ± 7.8	78.6 ± 2.9	10.3 ± 9.7	21.2 ± 7.7
B. kriegeri	19.8 ± 7.0	16.6 ± 2.6	90.0 ± 9.4	78.8 ± 7.6

Slight deviations from 100% at DAP 42 and 63 are due to rounding errors. Several other parasitoids account for missing percentages at DAP 49. DAP 56 yielded one *P. leucobasis* and one *B. kriegeri* and were not included in the analysis. No clear trend was found on the first and second order polynomial.

Table 4.33. Lema, season I/97, larval mortality of *M. sjostedti* in flowers due to parasitism, comparison of 2 NPK levels (without/ with NPK) on 5 sampling days (DAP 42-70). Values are mean percentage ± SEM (detransformed from logit), (n) = number of larvae on which mortality is based, n = observations used, trials = number of larvae investigated for parasitism; trends in NPK, n = 77, trials = 7,442, $c^2 = 16.5^{[l]}$, df = 4, $P < 0.01$.

DAP	**42**	**49**	**56**	**63**	**70**
NPK					
Without	1.6 ± 0.6	3.5 ± 0.5	10.6 ± 1.0	4.0 ± 0.6	1.4 ± 0.5
(n)	(404)	(1,385)	(978)	(1,072)	(633)
With	9.8 ± 1.4	9.9 ± 0.9	20.1 ± 1.7	6.8 ± 1.2	0.7 ± 0.7
(n)	(487)	(1,182)	(568)	(569)	(164)

Table 4.34. IITA, season II/95, egg mortality of *M. vitrata* on carrier plants due to parasitism, comparison of 3 mulch types, *S. siamea*, *I. cylindrica* and *A. indica* against a control on 3 sampling days (DAP 63-77). Values are mean percentage ± SEM (detransformed from logit), (n) = number of eggs on which mortality is based, n = observations used, trials = number of eggs investigated for parasitism; trend on mulch profiles, n = 36, trials = 558, $c^2 = 42.5$, df = 6, $P << 0.01$.

DAP	**63**	**70**	**77**
Mulch			
Control	45.5 ± 15.0	31.4 ± 5.0	16.7 ± 4.4
(n)	(11)	(86)	(72)
S. siamea	50.0 ± 15.8	0.0 ± 0.0	26.4 ± 6.1
(n)	(10)	(42)	(53)
I. cylindrica	18.2 ± 11.6	13.0 ± 3.8	7.4 ± 3.6
(n)	(11)	(77)	(54)
A. indica	99.8 ± 0.2	6.1 ± 3.4	14.1 ± 3.8
(n)	(8)	(49)	(85)

Table 4.35. IITA, season I/96, egg mortality of *M. vitrata* on carrier plants due to parasitism, comparison of 3 mulch types, *S. siamea*, *I. cylindrica* and *A. indica* against a control on 6 sampling days (DAP 28, 35, 42, 56, 63, 70). Values are mean percentage ± SEM (detransformed from logit), (n) = number of eggs on which mortality is based, n = observations used, trials = number of eggs investigated for parasitism; trend on mulch profiles, n = 47, trials = 885, c^2 = 115.5, df = 9, $P << 0.01$.

DAP	**28**	**35**	**42**	**56**	**63**	**70**
Mulch						
Control	45.0 ± 5.6	27.2 ± 6.7	27.9 ± 5.4	5.6 ± 5.4	0.0 ± 0.0	0.0 ± 0.0
(n)	(80)	(44)	(68)	(18)	(21)	(145)
S. siamea	16.2 ± 4.3	28.2 ± 5.3	54.2 ± 7.2	23.1 ± 8.3	0.0 ± 0.0	0.0 ± 0.0
(n)	(74)	(71)	(48)	(26)	(14)	(147)
I. cylindrica	8.0 ± 3.1	48.2 ± 5.5	1.7 ± 1.7	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
(n)	(75)	(83)	(59)	(9)	(17)	(198)
A. indica	40.4 ± 5.2	64.3 ± 5.7	4.8 ± 2.7	50.0 ± 17.7	0.0 ± 0.0	0.0 ± 0.0
(n)	(89)	(70)	(63)	(8)	(17)	(103)

At DAP 49 no eggs could be obtained from the permanent *M. vitrata* population that had collapsed temporarily.

Table 4.36. IITA, season I/97, egg mortality of *M. vitrata* on carrier plants due to parasitism, comparison of 3 mulch types, *S. siamea*, *I. cylindrica* and *A. indica* against a control on 3 sampling days (DAP 42-56). Values are mean percentage ± SEM (detransformed from logit), (n) = number of eggs on which mortality is based, n = observations used, trials = number of eggs investigated for parasitism; mulch main effect, n = 36, trials = 924, c^2 = 52.6, df = 3, $P << 0.01$; trend on mulch profiles, c^2 = 23.3, df = 6, $P < 0.01$.

DAP	**42**	**49**	**56**
Mulch			
Control	34.2 ± 5.4	8.6 ± 2.4	25.3 ± 5.8
(n)	(76)	(140)	(57)
S. siamea	51.1 ± 7.5	38.6 ± 4.3	67.6 ± 7.7
(n)	(45)	(127)	(37)
I. cylindrica	23.1 ± 5.0	23.4 ± 5.3	16.3 ± 5.3
(n)	(65)	(64)	(49)
A. indica	47.1 ± 5.3	19.4 ± 3.4	17.1 ± 5.9
(n)	(89)	(134)	(41)

Table 4.37. Parasitism in flowers of cowpea by three parasitoids *Dolichogenidea* sp., *Phanerotoma leucobasis* and *Braunsia kriegeri*. Proportion of the five instars attacked by each parasitoid species across 5 seasons in total and per region: Tokpa/Ayou, Lema and IITA. Total larvae = number of parasitized larvae across regions and seasons, (n) = number of parasitized larvae, (%) = proportion of attacks among the five larval instars.

***Dolichogenidea* sp.**

Instar	**1**	**2**	**3**	**4**	**5**	**Total**
Total larvae (n)	128	14	1	0	2	**145**
(%)	(88.3)	(9.7)	(0.7)	(0.0)	(1.4)	
Region						
Tokpa/Ayou (n)	3	1	0	0	0	**4**
	(75.0)	(25.0)	(0.0)	(0.0)	(0.0)	
Lema (n)	125	11	1	0	2	**139**
	(89.9)	(7.9)	(0.7)	(0.0)	(1.4)	
IITA (n)	0	2	0	0	0	**2**
	(0.0)	(100.0)	(0.0)	(0.0)	(0.0)	

Phanerotoma leucobasis

Instar	**1**	**2**	**3**	**4**	**5**	**Total**
Total larvae (n)	53	484	296	5	0	**838**
(%)	(6.3)	(57.8)	(35.3)	(0.6)	(0.0)	
Region						
Tokpa/Ayou (n)	1	32	31	0	0	**64**
	(1.6)	(50.0)	(48.4)	(0.0)	(0.0)	
Lema (n)	52	446	264	5	0	**767**
	(6.8)	(58.1)	(34.4)	(0.7)	(0.0)	
IITA (n)	0	6	1	0	0	**7**
	(0.0)	(85.7)	(14.3)	(0.0)	(0.0)	

Braunsia kriegeri

Instar	**1**	**2**	**3**	**4**	**5**	**Total**
Total larvae (n)	0	2	19	120	141	**282**
(%)	(0.0)	(0.7)	(6.7)	(42.6)	(50.0)	
Region						
Tokpa/Ayou (n)	0	0	1	21	33	**55**
	(0.0)	(0.0)	(1.8)	(38.2)	(60.0)	
Lema (n)	0	2	15	92	98	**207**
	(0.0)	(1.0)	(7.2)	(44.4)	(47.3)	
IITA (n)	0	0	3	7	10	**20**
	(0.0)	(0.0)	(15.0)	(35.0)	(50.0)	

Table 4.38. Parasitism in pods of cowpea by three parasitoids *Dolichogenidea* sp., *Phanerotoma leucobasis* and *Braunsia kriegeri*. Proportion of the five instars attacked by each parasitoid species across 5 seasons in total and per region: Tokpa/Ayou, Lema and IITA. Total larvae = number of parasitized larvae across regions and seasons, (n) = number of parasitized larvae, (%) = proportion of attacks among the five larval instars.

***Dolichogenidea* sp.**

Instar	**1**	**2**	**3**	**4**	**5**	**Total**
Total larvae (n)	6	2	0	0	1	**9**
(%)	(66.7)	(22.2)	(0.0)	(0.0)	(11.1)	
Region						
Tokpa/Ayou (n)	0	1	0	0	0	**1**
	(0.0)	(100.0)	(0.0)	(0.0)	(0.0)	
Lema (n)	6	1	0	0	1	**8**
	(75.0)	(12.5)	(0.0)	(0.0)	(12.5)	
IITA (n)	0	0	0	0	0	**0**
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	

Phanerotoma leucobasis

Instar	**1**	**2**	**3**	**4**	**5**	**Total**
Total larvae (n)	0	9	9	0	0	**18**
(%)	(0.0)	(50.0)	(50.0)	(0.0)	(0.0)	
Region						
Tokpa/Ayou (n)	0	2	4	0	0	**6**
	(0.0)	(33.3)	(66.7)	(0.0)	(0.0)	
Lema (n)	0	7	4	0	0	**11**
	(0.0)	(63.6)	(36.4)	(0.0)	(0.0)	
IITA (n)	0	0	1	0	0	**1**
	(0.0)	(0.0)	(100.0)	(0.0)	(0.0)	

Braunsia kriegeri

Instar	**1**	**2**	**3**	**4**	**5**	**Total**
Total larvae (n)	0	0	2	17	41	**60**
(%)	(0.0)	(0.0)	(3.3)	(28.3)	(68.3)	
Region						
Tokpa/Ayou (n)	0	0	0	7	17	**24**
	(0.0)	(0.0)	(0.0)	(29.2)	(70.8)	
Lema (n)	0	0	2	6	19	**27**
	(0.0)	(0.0)	(7.4)	(22.2)	(70.4)	
IITA (n)	0	0	0	4	5	**9**
	(0.0)	(0.0)	(0.0)	(44.4)	(55.6)	

Table 5.1. Mean number of pods on 10 plants per treatment, comparison of regions IITA, Lema and Tokpa/Ayou on 5 seasons ((√p + 3/8) transformed), region*season interaction, n = 674, $F_{(8,30)}$ = 8.4, $P << 0.01$.

Season	I/95	II/95	I/96	II/96	I/97
Region					
IITA	11.4 ± 0.8a[1]	3.4 ± 0.8a	10.1 ± 0.8a	5.3 ± 0.8a	10.5 ± 0.8a
Lema	3.9 ± 0.07b	3.3 ± 0.7a	8.0 ± 0.7b	5.6 ± 0.7a	4.7 ± 0.7b
Tokpa/Ayou	11.0 ± 0.7a	3.7 ± 0.7a	11.6 ± 0.7a	4.6 ± 0.7a	9.7 ± 0.7a

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.

Table 5.2. Mean weight of pods (g) on 10 plants per treatment, comparison of regions IITA, Lema and Tokpa/Ayou on 3 seasons (I/96, II/96, I/97) ((√p + 3/8) transformed), region*season interaction, n = 385, $F_{(4,18)}$ = 10.6, $P << 0.01$.

Season	I/96	II/96	I/97
Region			
IITA	4.9 ± 0.8b[1]	2.7 ± 0.9ab	6.9 ± 0.9a
Lema	4.0 ± 0.6b	3.8 ± 0.6a	1.8 ± 0.7b
Tokpa/Ayou	8.3 ± 0.6a	2.0 ± 0.6b	6.2 ± 0.6a

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.

Table 5.3. Weight per pod (g) on 10 plants per treatment, comparison of regions IITA, Lema and Tokpa/Ayou on 3 seasons (I/96, II/96, I/97) ((√p + 3/8) transformed), region*season interaction, n = 385, $F_{(4,18)}$ = 13.9, $P << 0.01$.

Season	I/96	II/96	I/97
Region			
IITA	0.8 ± 0.04b[1]	0.8 ± 0.05b	0.9 ± 0.05a
Lema	0.8 ± 0.03b	0.9 ± 0.03a	0.7 ± 0.03b
Tokpa/Ayou	0.9 ± 0.03a	0.7 ± 0.03b	0.9 ± 0.03a

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.

Table 5.4. Pod damage in cowpea by *M. vitrata*, comparison of regions IITA, Lema and Tokpa/Ayou across seasons. Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of pods on which damage is based, n = observations used, trials = number of pods investigated for damage; comparison of mulch types *S. siamea* and *I. cylindrica* against the control among regions, n = 511, trials = 42,105, $c^2 = 29.8$, df = 4, $P < 0.05$.

Mulch	**Control**	***S. siamea***	***I. cylindrica***
Region			
IITA	12.8 ± 0.6	9.8 ± 0.5	12.9 ± 0.6
(n)	(2,995)	(3,028)	(3,009)
Lema	9.4 ± 0.5	11.9 ± 0.6	11.8 ± 0.7
(n)	(3,626)	(2,609)	(2,545)
Tokpa/Ayou	11.2 ± 0.3	10.3 ± 0.4	10.9 ± 0.3
(n)	(8,908)	(7,595)	(7,790)

Table 5.5. Estimated yield loss ascribed to *M. vitrata*, comparison of regions IITA, Lema and Tokpa/Ayou over 5 seasons (arcsine √p transformed ± SEM); region*season interaction, n = 634, $F_{(8,30)} = 17.1$, $P << 0.01$.

Season	**I/95**	**II/95**	**I/96**	**II/96**	**I/97**
Region					
IITA	0.17 ± 0.021a[1]	0.02 ± 0.021a	0.15 ± 0.021a	0.01 ± 0.025b	0.17 ± 0.025b
Lema	0.04 ± 0.017b	0.00 ± 0.000a	0.15 ± 0.016a	0.19 ± 0.016a	0.07 ± 0.019c
Tokpa/Ayou	0.11 ± 0.016b	0.02 ± 0.017a	0.18 ± 0.015a	0.03 ± 0.016b	0.26 ± 0.016a

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.

Table 5.6. Tokpa/Ayou, mean number of pods on 10 plants per treatment ((√p + 3/8) transformed) on 2 NPK levels (without/ with) and 5 seasons; NPK main effect, n = 287, $F_{(1,247)} = 14.0$, $P < 0.01$; season main effect, $F_{(4,10)} = 50.3$, $P < 0.01$.

Season	**I/95**	**II/95**	**I/96**	**II/96**	**I/97**
NPK					
Without	10.5 ± 0.7A[1]	3.4 ± 0.7C	10.9 ± 0.6A	3.9 ± 0.7C	8.8 ± 0.7B
With	11.5 ± 0.7A	4.0 ± 0.7B	12.2 ± 0.6A	5.3 ± 0.7B	10.7 ± 0.7A

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 5.7. Tokpa/Ayou, pod damage in cowpea by *M. vitrata* during 5 seasons on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control. Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of pods on which damage is based, n = observations used, trials = number of pods investigated for damage; a) Season*NPK interaction, n = 282, trials = 25,287, c^2 = 17.5, df = 4, $P < 0.01$; b) Season*mulch interaction, c^2 = 18.8, df = 8, $P < 0.05$.

a) Season	**I/95**	**II/95**	**I/96**	**II/96**	**I/97**
NPK					
Without	7.5 ± 0.5B[1]	2.6 ± 0.9D	6.2 ± 0.3C	1.4 ± 0.5D	22.7 ± 0.9A
(n)	(3,106)	(423)	(4,841)	(476)	(2,185)
With	8.6 ± 0.5B	0.7 ± 0.3E	5.8 ± 0.3C	2.6 ± 0.5D	27.5 ± 0.8A
(n)	(3,530)	(571)	(6,066)	(890)	(3,199)

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

b) Season	**I/95**	**II/95**	**I/96**	**II/96**	**I/97**
Mulch					
Control	7.5 ± 0.6	2.1 ± 0.8	6.1 ± 0.4	2.1 ± 0.7	26.6 ± 0.9
(n)	(2,191)	(393)	(4,064)	(450)	(2,203)
S. siamea	7.4 ± 0.6	0.7 ± 0.4	6.0 ± 0.4	0.9 ± 0.5	25.4 ± 1.2
(n)	(2,240)	(344)	(3,662)	(326)	(1,367)
I. cylindrica	9.6 ± 0.6	1.5 ± 0.9	5.8 ± 0.4	3.1 ± 0.7	24.0 ± 1.0
(n)	(2,205)	(257)	(3,181)	(590)	(1,814)

Table 5.8. Lema, pod damage in cowpea by *M. vitrata* during 4 seasons (I/95, I/96, II/96, I/97) on 2 mulch types, *S. siamea* and *I. cylindrica*, against the control. Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of pods on which damage is based, n = observations used, trials = number of pods investigated for damage; season main effect, n = 190, trials = 8,780, c^2 = 183.7, df = 3, *P* << 0.01; season*mulch interaction, c^2 = 13.6, df = 6, *P* < 0.05.

Season	**I/95**	**I/96**	**II/96**	**I/97**
Mulch				
Control	3.9 ± 0.9	11.7 ± 1.0	20.3 ± 1.4	4.1 ± 0.6
(n)	(541)	(1,140)	(858)	(1,087)
S. siamea	3.5 ± 1.0	10.2 ± 0.8	24.0 ± 1.8	3.5 ± 1.0
(n)	(324)	(1,246)	(587)	(452)
I. cylindrica	1.4 ± 0.7	11.7 ± 0.8	15.4 ± 1.5	2.4 ± 1.1
(n)	(284)	(1,429)	(585)	(247)

Season II/95 was discarded from analysis due to some rare events of damage.

Table 5.9. Lema, grain damage of cowpea by *M. vitrata* during 4 seasons (I/95, I/96, II/96, I/97) on 2 mulch types, *S. siamea* and *I. cylindrica*, against the control. Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of grains on which damage is based, n = observations used, trials = number of grains investigated for damage; season*mulch interaction, n = 121, trials = 12,5583, c^2 = 47.2, df = 6, *P* << 0.01.

Season	**I/95**	**I/96**	**II/96**	**I/97**
Mulch				
Control	21.3 ± 3.4	37.1 ± 3.1	28.7 ± 2.7	25.3 ± 3.5
(n)	(7,724)	(17,872)	(14,658)	(14,006)
S. siamea	56.6 ± 8.5	27.4 ± 2.6	26.2 ± 2.8	33.9 ± 6.8
(n)	(1,313)	(21,133)	(9,146)	(4,531)
I. cylindrica	68.0 ± 7.8	27.0 ± 2.8	23.1 ± 2.9	33.3 ± 5.8
(n)	(1,166)	(23,190)	(9,145)	(1,699)

Season II/95 was discarded from analysis due to some rare events of damage.

Table 5.10. IITA, pod damage in cowpea by *M. vitrata* during 3 seasons (I/95, I/96, I/97) on 3 mulch types, *S. siamea*, *I. cylindrica* and *A. indica*, against the control. Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of pods on which damage is based, n = observations used, trials = number of pods investigated for damage; mulch main effect, n = 96, trials = 11,593, c^2 = 12.5, df = 3, $P < 0.01$; season*mulch interaction, c^2 = 12.8, df = 6, $P < 0.05$.

Season	**I/95**	**I/96**	**I/97**
Mulch			
Control	10.3 ± 0.9	15.6 ± 1.1	12.5 ± 1.4
(n)	(1,232)	(1,089)	(522)
S. siamea	10.2 ± 0.9	12.1 ± 1.1	10.1 ± 1.1
(n)	(1,235)	(816)	(787)
I. cylindrica	13.5 ± 1.0	14.5 ± 1.1	13.7 ± 1.3
(n)	(1,094)	(979)	(716)
A. indica	9.6 ± 0.9	14.1 ± 1.0	15.2 ± 1.3
(n)	(1,203)	(1,117)	(803)

Seasons II/95 and II/96 were not included in the analysis due to rare events of damage, season II/95 revealed below 2% pod damage and II/96 remained below 1% on the raw data.

Table 5.11. Tokpa/Ayou, season I/95, mean number of pods on 10 plants per treatment across 3 sampling weeks (DAP 56-70) (non-transformed); NPK*mulch effect, n = 53, $F_{(2,33)}$ = 4.2, $P < 0.05$.

Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	98.4 ± 12.7b[1]A[2]	115.0 ± 12.7aA	131.7 ± 12.7aA
With	145.0 ± 12.7aA	148.9 ± 13.8aA	113.3 ± 12.7aA

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.
Values are non-transformed means from analysis.

Table 5.12. Tokpa/Ayou, season I/95, pod damage in cowpea by *M. vitrata* on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control over 3 sampling weeks (DAP 56-70). Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of pods on which damage is based, n = observations used, trials = number of pods investigated for damage; a) NPK*mulch interaction, n = 53, trials = 6,636, c^2 = 10.4, df = 2, $P < 0.01$; b) trend on NPK profiles, c^2 = 9.5, df = 2, $P < 0.01$.

a) Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	7.2 ± 0.9	5.3 ± 0.8	5.8 ± 0.8
(n)	(886)	(1,035)	(1,185)
With	5.3 ± 0.7	4.6 ± 0.7	10.0 ± 1.1
(n)	(1,305)	(1,205)	(1,020)

b) DAP	**56**	**63**	**70**
NPK			
Without	3.6 ± 0.8	7.7 ± 0.9	6.6 ± 0.7
(n)	(618)	(1,259)	(1,229)
With	6.0 ± 0.8	8.1 ± 0.8	5.2 ± 0.8
(n)	(913)	(1,447)	(1,170)

Table 5.13. Tokpa/Ayou, season I/96, pod damage in cowpea by *M. vitrata* on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control over 3 sampling weeks (DAP 56-70). Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of pods on which damage is based, n = observations used, trials = number of pods investigated for damage; NPK*mulch*DAP interaction, n = 47, trials = 10,205, c^2 = 23.7, df = 4, $P << 0.01$.

	DAP	**56**	**63**	**70**
NPK	**Mulch**			
Without	**Control**	3.3 ± 0.8	8.6 ± 1.1	7.0 ± 1.0
	(n)	(458)	(662)	(673)
	S. siamea	5.1 ± 1.0	9.5 ± 1.2	5.3 ± 1.0
	(n)	(511)	(590)	(514)
	I. cylindrica	8.0 ± 1.4	4.3 ± 1.2	6.9 ± 1.2
	(n)	(374)	(304)	(447)
With	**Control**	5.3 ± 0.9	9.0 ± 1.1	5.8 ± 0.9
	(n)	(646)	(657)	(668)
	S. siamea	2.7 ± 0.8	5.7 ± 0.9	7.5 ± 0.9
	(n)	(404)	(647)	(827)
	I. cylindrica	2.0 ± 0.7	7.5 ± 1.0	7.2 ± 1.0
	(n)	(409)	(691)	(723)

Table 5.14. Tokpa/Ayou, season I/97, pod damage in cowpea by *M. vitrata* on 2 mulch types, *S. siamea* and *I. cylindrica*, against the control over 3 sampling weeks (DAP 56-70). Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of pods on which damage is based, n = observations used, trials = number of pods investigated for damage; mulch*DAP interaction, n = 49, trials = 5,384, c^2 = 13.7, df = 4, $P < 0.01$.

DAP	**56**	**63**	**70**
Mulch			
Control	5.4 ± 1.0	35.5 ± 2.1	26.1 ± 1.8
(n)	(554)	(828)	(821)
S. siamea	8.7 ± 1.5	43.8 ± 2.4	18.9 ± 1.7
(n)	(341)	(471)	(555)
I. cylindrica	4.8 ± 1.0	38.5 ± 2.0	23.4 ± 2.4
(n)	(452)	(623)	(739)

Table 5.15. Tokpa/Ayou, season I/97, pod damage in cowpea by *M. vitrata* on 2 mulch types, *S. siamea* and *I. cylindrica*, against the control over 3 sampling weeks (DAP 56-70). Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of pods on which damage is based, n = observations used, trials = number of pods investigated for damage; mulch main effect, n = 46, trials = 1,149, c^2 = 7.0, df = 2, $P < 0.05$; mulch*DAP interaction, c^2 = 14.5, df = 4, $P < 0.01$.

DAP	**56**	**63**	**70**
Mulch			
Control	2.3 ± 1.0	6.3 ± 1.9	4.5 ± 2.5
(n)	(285)	(182)	(74)
S. siamea	0.0 ± 0.0	2.1 ± 1.4	60.8 ± 1.7
(n)	(93)	(153)	(78)
I. cylindrica	0.0 ± 0.0	1.5 ± 1.5	3.1 ± 1.8
(n)	(112)	(72)	(100)

Table 5.16. Lema, season I/96, pod damage in cowpea by *M. vitrata* on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control over 3 sampling weeks (DAP 49-63). Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of pods on which damage is based, n = observations used, trials = number of pods investigated for damage; NPK*mulch*DAP interaction, n = 54, trials = 3,815, c^2 = 16.2, df = 4, $P < 0.01$.

	DAP	**49**	**56**	**63**
NPK	**Mulch**			
Without	**Control**	0.0 ± 0.0	6.1 ± 1.5	8.3 ± 1.8
	(n)	(94)	(244)	(241)
	S. siamea	6.8 ± 3.8	13.1 ± 2.8	5.1 ± 1.5
	(n)	(44)	(145)	(215)
	I. cylindrica	0.0 ± 0.0	14.2 ± 2.4	4.7 ± 1.3
	(n)	(76)	(212)	(256)
With	**Control**	9.0 ± 2.9	32.1 ± 3.2	6.3 ± 1.5
	(n)	(100)	(209)	(252)
	S. siamea	8.0 ± 2.1	23.8 ± 2.7	6.7 ± 1.2
	(n)	(175)	(248)	(419)
	I. cylindrica	7.7 ± 1.7	31.2 ± 2.6	5.0 ± 1.2
	(n)	(235)	(311)	(339)

Table 5.17. Lema, season I/96, grain damage of cowpea by *M. vitrata* on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control over 3 sampling weeks (DAP 49-63). Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of grains on which damage is based, n = observations used, trials = number of grains investigated for damage; NPK*mulch*DAP interaction, n = 54, trials = 62,195, c^2 = 18.8, df = 4, $P < 0.01$.

	DAP	**49**	**56**	**63**
NPK	**Mulch**			
Without	**Control**	0.0 ± 0.0	24.2 ± 6.0	46.1 ± 6.8
	(n)		(4,121)	(4,268)
	S. siamea	24.0 ± 5.8	23.5 ± 6.1	23.2 ± 5.9
	(n)	(486)	(2,298)	(3,786)
	I. cylindrica	0.0 ± 0.0	24.6 ± 6.1	30.8 ± 6.4
	(n)		(3,490)	(4,561)
With	**Control**	15.6 ± 4.9	38.9 ± 6.8	48.0 ± 6.9
	(n)	(1,569)	(3,554)	(4,360)
	S. siamea	17.6 ± 5.2	37.6 ± 7.1	30.4 ± 6.3
	(n)	(3,174)	(3,885)	(7,504)
	I. cylindrica	15.4 ± 4.9	31.3 ± 6.5	35.1 ± 6.8
	(n)	(4,179)	(5,257)	(5,703)

Number of grains for the control and *Imperata* without NPK fertilizer were not recorded since this was done in attacked pods only.

Table 5.18. Lema, season I/96, estimated yield loss ascribed to *M. vitrata* on 2 NPK levels (without/ with) over 3 sampling weeks (DAP 49-63) (arcsine √p transformed ± SEM); NPK main effect, n = 634, $F_{(1,34)} = 13.2$, $P < 0.01$, trend on NPK, $F_{(2,34)} = 6.0^{[q]}$, $P < 0.01$.

DAP	**49**	**56**	**63**
NPK			
Without	0.05 ± 0.02	0.16 ± 0.02	0.15 ± 0.02
With	0.11 ± 0.02	0.31 ± 0.02	0.15 ± 0.02

Table 5.19. Weight per pod (g) on 10 plants per treatment, 2 mulch types, *S. siamea* and *I. cylindrica*, against the control over 3 sampling weeks (DAP 49-63) (non-transformed data from analysis); mulch main effect, n = 54, $F_{(2,34)} = 9.9$, $P < 0.01$; trend on mulch, $F_{(4,34)} = 6.5^{[1]}$, $P < 0.01$.

DAP	**49**	**56**	**63**
Mulch			
Control	0.03 ± 0.096	0.61 ± 0.096	1.30 ± 0.096
S. siamea	0.03 ± 0.096	0.44 ± 0.096	1.33 ± 0.096
I. cylindrica	0.02 ± 0.096	0.27 ± 0.096	0.54 ± 0.096

Table 5.20. Lema, season II/96, pod damage in cowpea by *M. vitrata* on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control over 3 sampling weeks (DAP 49-63). Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of pods on which damage is based, n = observations used, trials = number of pods investigated for damage; NPK*mulch*DAP interaction, n = 53, trials = 2,030, $c^2 = 13.8$, df = 4, $P < 0.01$.

	DAP	**49**	**56**	**63**
NPK	**Mulch**			
Without	**Control**	5.0 ± 3.4	26.8 ± 6.9	24.0 ± 4.3
	(n)	(40)	(41)	(100)
	S. siamea	2.0 ± 2.0	8.0 ± 3.8	45.7 ± 7.3
	(n)	(49)	(50)	(46)
	I. cylindrica	0.0 ± 0.0	21.2 ± 7.1	8.7 ± 2.9
	(n)	(29)	(33)	(92)
With	**Control**	8.6 ± 1.9	28.6 ± 2.8	29.3 ± 3.2
	(n)	(220)	(259)	(198)
	S. siamea	5.4 ± 1.9	33.9 ± 4.3	40.9 ± 3.8
	(n)	(147)	(124)	(171)
	I. cylindrica	1.6 ± 1.1	25.6 ± 4.0	26.7 ± 3.2
	(n)	(127)	(117)	(187)

Table 5.21. Lema, season II/96, grain damage of cowpea by *M. vitrata* on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control over 3 sampling weeks (DAP 49-63). Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of grains on which damage is based, n = observations used, trials = number of grains investigated for damage; NPK*mulch*DAP interaction, n = 54, trials = 32,948, c^2 = 9.9, df = 4, $P < 0.05$.

	DAP	**49**	**56**	**63**
NPK	**Mulch**			
Without	**Control**	23.9 ± 5.9	19.7 ± 5.4	27.7 ± 6.3
	(n)	(493)	(733)	(1,689)
	S. siamea	3.8 ± 2.6	12.5 ± 4.5	26.7 ± 6.3
	(n)	(468)	(640)	(747)
	I. cylindrica	0.0 ± 0.0	24.1 ± 5.8	17.6 ± 5.3
	(n)		(602)	(1,429)
With	**Control**	27.7 ± 6.2	23.7 ± 5.8	29.6 ± 6.5
	(n)	(3,852)	(4,582)	(3,310)
	S. siamea	9.4 ± 4.0	38.3 ± 6.6	32.8 ± 6.6
	(n)	(2,117)	(2,220)	(2,953)
	I. cylindrica	13.0 ± 4.6	21.3 ± 5.6	17.5 ± 5.3
	(n)	(1,764)	(2,071)	(3,278)

Number of grains for the control without NPK fertilizer was not recorded since this was done in attacked pods only.

Table 5.22. Lema, season II/96, estimated yield loss ascribed to *M. vitrata* on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control over 3 sampling weeks (DAP 49-63) (arcsine √p transformed ± SEM); NPK*mulch*DAP interaction, n = 53, $F_{(4,33)} = 3.1$, $P < 0.05$.

	DAP	49	56	63
NPK	**Mulch**			
Without	**Control**	0.08 ± 0.06	0.22 ± 0.06	0.26 ± 0.06
	S. siamea	0.02 ± 0.06	0.09 ± 0.06	0.37 ± 0.06
	I. cylindrica	0.00 ± 0.00	0.23 ± 0.06	0.10 ± 0.06
With	**Control**	0.15 ± 0.06	0.26 ± 0.06	0.29 ± 0.06
	S. siamea	0.06 ± 0.06	0.42 ± 0.06	0.41 ± 0.06
	I. cylindrica	0.05 ± 0.06	0.21 ± 0.06	0.26 ± 0.07

Table 5.23. Lema, season I/97, pod damage in cowpea by *M. vitrata* on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control over 3 sampling weeks (DAP 56-70). Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of pods on which damage is based, n = observations used, trials = number of pods investigated for damage; a) trend on NPK, n = 37, trials = 1,786, $c^2 = 6.6$, df = 2, $P < 0.05$; b) trend on mulch, $c^2 = 10.4$, df = 4, $P < 0.05$.

a) DAP	**56**	**63**	**70**
NPK			
Without	6.3 ± 1.4	2.0 ± 0.6	4.9 ± 1.0
(n)	(306)	(496)	(514)
With	8.4 ± 3.0	0.0 ± 0.0	2.1 ± 1.8
(n)	(204)	(163)	(103)

b) DAP	**56**	**63**	**70**
Mulch			
Control	7.3 ± 1.7	0.9 ± 0.5	4.9 ± 1.1
(n)	(318)	(396)	(373)
S. siamea	8.0 ± 3.3	3.4 ± 1.3	1.9 ± 1.0
(n)	(110)	(157)	(185)
I. cylindrica	2.6 ± 1.8	0.7 ± 0.7	5.0 ± 3.5
(n)	(82)	(106)	(59)

Table 5.24. IITA, season I/95, pod damage in cowpea by *M. vitrata* on 3 mulch types, *S. siamea*, *I. cylindrica* and *A. indica*, against the control over 3 sampling weeks (DAP 56-70). Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of pods on which damage is based, n = observations used, trials = number of pods investigated for damage; trend on mulch, n = 36, trials = 4,764, $c^2 = 18.8^{[q]}$, df = 6, $P < 0.01$.

DAP	56	63	70
Mulch			
Control	15.0 ± 1.8	10.1 ± 1.4	6.1 ± 1.2
(n)	(374)	(464)	(394)
S. siamea	12.3 ± 1.8	14.1 ± 1.5	2.9 ± 0.9
(n)	(341)	(516)	(378)
I. cylindrica	19.3 ± 2.1	18.1 ± 2.1	5.2 ± 1.1
(n)	(347)	(326)	(421)
A. indica	9.2 ± 2.1	15.5 ± 1.8	4.1 ± 1.0
(n)	(415)	(399)	(389)

Table 5.25. IITA, season I/96, pod damage in cowpea by *M. vitrata* on 3 mulch types, *S. siamea*, *I. cylindrica* and *A. indica*, against the control over 3 sampling weeks (DAP 49-63). Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of pods on which damage is based, n = observations used, trials = number of pods investigated for damage; trend on mulch, n = 36, trials = 4,001, $c^2 = 12.7$, df = 6, $P < 0.05$.

DAP	49	56	63
Mulch			
Control	2.2 ± 0.9	12.4 ± 1.6	29.5 ± 2.4
(n)	(275)	(444)	(370)
S. siamea	0.0 ± 0.0	9.1 ± 1.6	21.8 ± 2.3
(n)	(181)	(309)	(326)
I. cylindrica	0.0 ± 0.0	13.7 ± 1.8	22.5 ± 2.1
(n)	(205)	(365)	(409)
A. indica	1.0 ± 0.7	9.8 ± 1.4	23.4 ± 1.9
(n)	(194)	(440)	(483)

Table 5.26. IITA, season I/97, pod damage in cowpea by *M. vitrata* on 3 mulch types, *S. siamea*, *I. cylindrica* and *A. indica*, against the control over 2 sampling weeks (DAP 56, 63). Values are mean percentage ± SEM on 10 plants per treatment (detransformed from logit), (n) = number of pods on which damage is based, n = observations used, trials = number of pods investigated for damage; mulch main effect, n = 24, trials = 2,828, $c^2 = 11.8$, df = 3, $P < 0.01$; trend on mulch, $c^2 = 8.5$, df = 3, $P < 0.05$.

DAP	**56**	**63**
Mulch		
Control	7.6 ± 1.6	18.0 ± 2.5
(n)	(278)	(244)
S. siamea	6.0 ± 1.2	15.1 ± 1.9
(n)	(429)	(358)
I. cylindrica	10.7 ± 1.7	16.3 ± 1.9
(n)	(336)	(380)
A. indica	13.9 ± 1.6	16.9 ± 2.0
(n)	(454)	(349)

Table 6.1. Mean number of pods harvested on 50 plants per treatment ((√p + 3/8) transformed), comparison among 3 regions on 4 seasons (II/95, I/96, II/96, I/97), region*season interaction, n = 180, $F_{(6,24)} = 5.2$, $P < 0.01$.

Season	**II/95**	**I/96**	**II/96**	**I/97**
Region				
IITA	9.5 ± 1.9a[1]	25.2 ± 1.9b	10.4 ± 1.9a	22.9 ± 1.9a
Lema	5.2 ± 1.7a	26.8 ± 1.7b	14.0 ± 1.7a	11.6 ± 1.7b
Tokpa/Ayou	9.7 ± 1.7a	34.6 ± 1.7a	14.5 ± 1.7a	25.4 ± 1.7a

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
Pod numbers were counted beginning with season II/95.

Table 6.2. Mean weight per pod (g) on 50 plants per treatment ((√p + 3/8) transformed), comparison among 3 regions on 4 seasons (II/95, I/96, II/96, I/97), region*season interaction, n = 180, $F_{(6,24)} = 22.2$, $P << 0.01$; (g pod^{-1}) = detransformed means of 50 plants per treatment.

Season	**II/95**	**I/96**	**II/96**	**I/97**
Region				
IITA	0.83 ± 0.05a[1]	1.04 ± 0.05b	1.09 ± 0.05a	1.13 ± 0.05a
(g pod^{-1})	(0.32)	(0.71)	(0.82)	(0.91)
Lema	0.65 ± 0.04b	0.98 ± 0.04b	1.19 ± 0.04a	0.73 ± 0.04b
(g pod^{-1})	(0.05)	(0.59)	(1.04)	(0.16)
Tokpa/Ayou	0.61 ± 0.04b	1.33 ± 0.04a	0.78 ± 0.04b	1.19 ± 0.04a
(g pod^{-1})	(0.00)	(1.39)	(0.24)	(1.03)

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
Pod numbers were weighed beginning with season II/95.

Table 6.3. Mean yield of pods and grains (dry matter in g) harvested on 50 plants per treatment ((√p + 3/8) transformed), comparison among 3 regions on 5 seasons, region*season interaction; a) Pod yield, n = 225, $F_{(8,30)} = 23.6$, $P << 0.01$; b) Grain yield, $F_{(8,30)} = 24.6$, $P << 0.01$, (kg ha^{-1}) = means of 50 plants per treatment were extrapolated to yields per hectare on known plant numbers per treatment.

a) Season	**I/95**	**II/95**	**I/96**	**II/96**	**I/97**
Region					
IITA	34.3 ± 2.2b[1]	5.4 ± 2.2a	21.6 ± 2.2b	9.6 ± 2.2b	22.0 ± 2.2b
Lema	5.6 ± 2.0c	1.9 ± 2.0c	19.9 ± 2.0c	14.5 ± 2.0a	5.0 ± 2.0c
Tokpa/Ayou	43.8 ± 2.0a	3.4 ± 2.0b	40.8 ± 2.0a	7.1 ± 2.0c	26.0 ± 2.0a

b) Season / Region	I/95	II/95	I/96	II/96	I/97
IITA	26.4 ± 1.9b[1]	2.8 ± 2.2a	17.2 ± 1.9b	7.1 ± 1.9ab	17.3 ± 1.9a
(kg ha^{-1})	(736.1)	(7.8)	(317.6)	(54.4)	(322.2)
Lema	3.6 ± 1.8c	0.6 ± 1.8a	14.7 ± 1.8b	11.6 ± 1.8a	2.3 ± 1.8b
(kg ha^{-1})	(12.4)	(0.0)	(183.3)	(114.4)	(4.8)
Tokpa/Ayou	36.2 ± 1.8a	0.7 ± 1.8a	35.5 ± 1.8a	3.7 ± 1.8b	20.7 ± 1.8a
(kg ha^{-1})	(1,046.0)	(0.1)	(1,014.8)	(10.4)	(342.2)

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.

Table 6.4. Mean number of pods harvested on 50 plants per treatment ($(\sqrt{p} + 3/8)$ transformed), comparison among 2 on-farm regions on 2 NPK levels (without/ with) in 4 seasons (II/95, I/96, II/96, I/97), region*season*NPK interaction, n = 144, $F_{(3,86)} = 5.2$, $P < 0.01$.

Season / Region	NPK	II/95	I/96	II/96	I/97
Lema	**Without**	5.4 ± 1.8a[1]	23.3 ± 1.8c	11.6 ± 1.8c	14.2 ± 1.8b
	With	5.0 ± 1.8a	30.3 ± 1.8b	16.4 ± 1.8ab	8.9 ± 1.8c
Tokpa/Ayou	**Without**	9.3 ± 1.8a	32.7 ± 1.8b	13.3 ± 1.8bc	24.7 ± 1.8a
	With	10.1 ± 1.8a	36.5 ± 1.8a	15.7 ± 1.8bc	26.2 ± 1.8a

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
Pod numbers were counted beginning with season II/95.

Table 6.5. Mean weight per pod (g) on 50 plants per treatment ($(\sqrt{p} + 3/8)$ transformed) on 2 NPK levels (without/ with) in 4 seasons (II/95, I/96, II/96, I/97) across 2 on-farm regions, season*NPK interaction, n = 144, $F_{(3,86)} = 3.8$, $P < 0.05$; (g pod^{-1}) = detransformed means of 50 plants per treatment.

Season / NPK	II/95	I/96	II/96	I/97
Without	0.64 ± 0.03a[1]C[2]	1.17 ± 0.03aA	0.95 ± 0.03bB	0.97 ± 0.03aB
(g pod^{-1})	(0.04)	(0.99)	(0.53)	(0.56)
With	0.62 ± 0.03aC	1.14 ± 0.03aA	1.02 ± 0.03aB	0.95 ± 0.03aB
(g pod^{-1})	(0.01)	(0.92)	(0.67)	(0.52)

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$
Pod weights were taken beginning with season II/95.

Table 6.6. Mean yield of pods (dry matter in g) harvested on 50 plants per treatment ((√p + 3/8) transformed) on 2 NPK levels (without/ with) in 5 seasons across 2 on-farm regions, season*NPK interaction; pod yield, n = 180, $F_{(4,108)} = 4.1$, $P < 0.01$.

Season	I/95	II/95	I/96	II/96	I/97
NPK					
Without	24.4 ± 1.4a[1]B[2]	2.8 ± 1.4aE	28.4 ± 1.4bA	8.6 ± 1.4bD	15.8 ± 1.4aC
With	25.0 ± 1.4aB	2.5 ± 1.4aE	32.2 ± 1.4aA	13.0 ± 1.4aC	15.2 ± 1.4aC

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 6.7. Tokpa/Ayou, mean number of pods harvested on 50 plants per treatment ((√p + 3/8) transformed) on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control among 4 seasons (II/95, I/96, II/96, I/97), season*NPK*mulch interaction, n = 72, $F_{(6,40)} = 2.5$, $P < 0.05$.

	Season	II/95	I/96	II/96	I/97
NPK	**Mulch**				
Without	**Control**	10.8 ± 2.0	32.7 ± 2.0	11.4 ± 2.0	28.1 ± 2.0
	S. siamea	9.8 ± 2.0	33.4 ± 2.0	15.5 ± 2.0	24.9 ± 2.0
	I. cylindrica	7.3 ± 2.0	32.0 ± 2.0	13.1 ± 2.0	21.2 ± 2.0
With	**Control**	9.4 ± 2.0	36.5 ± 2.0	18.5 ± 2.0	28.5 ± 2.0
	S. siamea	11.5 ± 2.0	37.1 ± 2.0	13.8 ± 2.0	22.5 ± 2.0
	I. cylindrica	9.4 ± 2.0	35.9 ± 2.0	14.9 ± 2.0	27.5 ± 2.0

Pod numbers were counted beginning with season II/95.

Table 6.8. Mean yield of pods and grains (dry matter in g) harvested on 50 plants per treatment ((√p + 3/8) transformed) on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control over 5 seasons across 2 on-farm regions, NPK*mulch interaction; a) Pod yield, n = 90, $F_{(2,50)} = 4.3$, $P < 0.05$; b) Grain yield, $F_{(2,50)} = 3.2$, $P < 0.05$; (kg ha^{-1}) = means of 50 plants per treatment were extrapolated to yields per hectare on known plant numbers per treatment.

a) Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	23.9 ± 0.8A[1]	23.3 ± 0.8A	22.5 ± 0.8A
With	26.0 ± 0.8A	23.6 ± 0.8B	25.9 ± 0.8A

b) Mulch / NPK	Control	*S. siamea*	*I. cylindrica*
Without	19.1 ± 0.7A[1]	18.6 ± 0.7A	18.1 ± 0.7A
(kg ha^{-1})	(295.8)	(280.7)	(266.6)
With	20.5 ± 0.7A	18.6 ± 0.7B	21.0 ± 0.7A
(kg ha^{-1})	(341.9)	(279.3)	(359.8)

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 6.9. Lema, mean number of pods harvested on 50 plants per treatment ($(\sqrt{p} + 3/8)$ transformed) on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control across 5 seasons, NPK*mulch interaction, n = 89, $F_{(2,49)} = 4.5$, $P < 0.05$.

Mulch / NPK	Control	*S. siamea*	*I. cylindrica*
Without	11.7 ± 1.1A[1]	12.7 ± 1.1A	10.8 ± 1.1A
With	15.5 ± 1.1A	11.5 ± 1.1B	10.9 ± 1.1B

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 6.10. Lema, mean yield of grains (dry matter in g) harvested on 50 plants per treatment ((√p + 3/8) transformed) on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control over 5 seasons; seasons*NPK*mulch interaction, n = 90, $F_{(8,50)} = 2.2$, $P < 0.05$; (kg ha^{-1}) = means of 50 plants per treatment were extrapolated to yields per hectare on known plant numbers per treatment.

	Season	**I/95**	**II/95**[2]	**I/96**	**II/96**	**I/97**
NPK	**Mulch**					
Without	**Control**	1.4 ± 2.5c[1]	0.0 ± 0.0	17.0 ± 2.5a	9.0 ± 2.5c	5.4 ± 2.5a
	(kg ha^{-1})	(1.6)	(0)	(246.8)	(68.1)	(27.9)
	S. siamea	5.4 ± 2.5cd	0.0 ± 0.0	11.4 ± 2.5b	10.3 ± 2.5bc	2.3 ± 2.5a
	(kg ha^{-1})	(28.8)	(0)	(109.9)	(89.9)	(4.8)
	I. cylindrica	1.6 ± 2.5c	0.0 ± 0.0	14.8 ± 2.5ab	6.6 ± 2.5c	1.4 ± 2.5a
	(kg ha^{-1})	(2.3)	(0)	(185.6)	(36.9)	(1.5)
With	**Control**	7.0 ± 2.5ad	0.0 ± 0.0	12.9 ± 2.5ab	19.1 ± 2.5a	3.5 ± 2.5a
	(kg ha^{-1})	(48.1)	(0)	(141.0)	(312.0)	(11.7)
	S. siamea	0.6 ± 2.5bd	0.0 ± 0.0	15.7 ± 2.5ab	15.1 ± 2.5ab	0.6 ± 2.5a
	(kg ha^{-1})	(0)	(0)	(210.5)	(193.9)	(0)
	I. cylindrica	5.4 ± 2.5abd	0.0 ± 0.0	16.3 ± 2.5ab	9.5 ± 2.5c	0.6 ± 2.5a
	(kg ha^{-1})	(29.1)	(0)	(226.3)	(76.9)	(0)

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Season II/95 yielded few underdeveloped pods, which never recorded any weight of grains per 50 plants when weighed to a precision of 0.0 g. Analysis was not possible for this season.

Table 6.11. IITA, mean yield of grains (dry matter in g) harvested on 50 plants per treatment ((√p + 3/8) transformed) on 3 mulch types, *S. siamea*, *I. cylindrica* and *A. indica*, against the control over 5 seasons; season effect, n = 60, $F_{(4,10)} = 14.2$, $P < 0.01$; (kg ha^{-1}) = means of 50 plants per treatment were extrapolated to yields per hectare on known plant numbers per treatment.

	I/95	**II/95**	**I/96**	**II/96**	**I/97**
Grain yield					
	25.9 ± 2.5A[1]	2.4 ± 2.5C	17.2 ± 2.5B	7.1 ± 2.5C	17.5 ± 2.5B
(kg ha^{-1})	(707.6)	(6.0)	(318.2)	(53.9)	(332.0)

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 6.12. Tokpa/Ayou, season I/95, mean yield of grains (dry matter in g) harvested on 50 plants per treatment (non-transformed) on 2 mulch types, *S. siamea* and *I. cylindrica*, against the control; mulch effect, n = 18, $F_{(2,10)} = 5.9$, $P < 0.05$; (kg ha^{-1}) = means of 50 plants per treatment were extrapolated to yields per hectare on known plant numbers per treatment.

Mulch	**Control**	***S. siamea***	***I. cylindrica***
Grain yield	1,177.9 ± 91.6B[1]	1,295.4 ± 91.6AB	1,471.2 ± 91.6A
(kg ha^{-1})	(942.3)	(1,036.4)	(1,176.9)

[1] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 6.13. Tokpa/Ayou, season I/96, mean weight per pod (g) on 50 plants per treatment (non-transformed) on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control; NPK*mulch interaction, n = 18, $F_{(2,10)} = 6.0$, $P < 0.05$.

Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	1.29 ± 0.04b[1]B[2]	1.37 ± 0.04aA	1.40 ± 0.04aA
With	1.44 ± 0.04aA	1.37 ± 0.04aA	1.43 ± 0.04aA

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 6.14. Tokpa/Ayou, season II/96, mean yield of grains (dry matter in g) harvested on 50 plants per treatment (non-transformed) on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control; n = 18, $P \geq 0.05$; (kg ha^{-1}) = means of 50 plants per treatment were extrapolated to yields per hectare on known plant numbers per treatment.

Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	14.0 ± 37.9	11.5 ± 37.9	6.8 ± 37.9
(kg ha^{-1})	(11.2)	(9.2)	(5.5)
With	60.2 ± 37.9	5.7 ± 37.9	75.5 ± 37.9
(kg ha^{-1})	(48.1)	(4.5)	(60.4)

No significant treatment effects were observed.

Table 6.15. Tokpa/Ayou, season I/97, mean number of pods harvested on 50 plants per treatment (non-transformed) on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control, NPK*mulch interaction, n = 18, $F_{(2,10)} = 12.8$, $P < 0.01$.

Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	787.7 ± 45.4a[1]A[2]	620.7 ± 45.4aB	451.0 ± 45.4bC
With	810.3 ± 45.4aA	512.0 ± 45.4aB	757.7 ± 45.4aA

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 6.16. Tokpa/Ayou, season I/97, mean yield of pods and grains (dry matter in g) harvested on 50 plants per treatment (non-transformed) on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control; a) Pod yield, NPK*mulch interaction, n = 18, $F_{(2,10)} = 10.6$, $P < 0.01$; b) Grain yield, mulch effect, $F_{(2,10)} = 7.1$, $P < 0.05$, (kg ha^{-1}) = means of 50 plants per treatment were extrapolated to yields per hectare on known plant numbers per treatment.

a) Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	911.8 ± 66.7a[1]A[2]	620.7 ± 66.7aB	437.3 ± 66.7bB
With	1,007.3 ± 66.7aA	417.0 ± 66.7bC	786.8 ± 66.7aB

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
2 Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

b) Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	627.8 ± 73.8	407.3 ± 73.8	277.5 ± 73.8
(kg ha^{-1})	(502.3)	(325.9)	(222.0)
With	574.3 ± 73.8	260.2 ± 73.8	523.0 ± 73.8
(kg ha^{-1})	(459.5)	(208.1)	(418.4)

Table 6.17. Lema, season I/96, mean weight per pod (g) on 50 plants per treatment (non-transformed) on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control; NPK*mulch interaction, n = 18, $F_{(2,10)} = 5.6$, $P < 0.05$.

Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	0.94 ± 0.2a[1]A[2]	0.51 ± 0.2aB	0.67 ± 0.2aB
With	0.43 ± 0.2bA	0.55 ± 0.2aA	0.58 ± 0.2aA

[1] Means followed by the same letter within each column are not significantly different at $P \geq 0.05$.
[2] Means followed by the same letter within each row are not significantly different at $P \geq 0.05$.

Table 6.18. Lema, season I/97, mean yield of grains (dry matter in g) harvested on 50 plants per treatment ($(\sqrt{p} + 3/8)$ transformed) on 2 NPK levels (without/ with) and 2 mulch types, *S. siamea* and *I. cylindrica*, against the control; NPK effect, n = 18, $F_{(1,10)} = 8.4$, $P < 0.05$; mulch effect, $F_{(2,10)} = 18.6$, $P < 0.01$; (kg ha^{-1}) = means of 50 plants per treatment were extrapolated to yields per hectare on known plant numbers per treatment.

Mulch	**Control**	***S. siamea***	***I. cylindrica***
NPK			
Without	5.4 ± 0.6	2.3 ± 0.6	1.4 ± 0.6
(kg ha^{-1})	(27.9)	(4.8)	(1.5)
With	3.5 ± 0.6	0.6 ± 0.6	0.6 ± 0.6
(kg ha^{-1})	(11.7)	(0.0)	(0.0)

Table 7.1. Larvae of *M. vitrata* encountered in wild host plants over a period of 2 ½ years (March 1995-August 1997) in three regions, Tokpa/Ayou, Lema and IITA. Maximum 50 flowers^{-1} = highest number of larvae collected in 50 flowers during one event; events = number of sampling times during the whole period where larvae were encountered; number of sampling weeks = number of weeks where flowers were sampled.

Host plant	Maximum 50 flowers^{-1}	Events	Number of sampling weeks
C. cajan[1]	5	3*	36
C. ensiflora[3]	1	1	4
C. pubescens[3]	2	2*	113
D. africanus[2]	26	3	7
E. senegalensis[2]	1	1	15
T. bracteolata[2]	4	3*	52
T. candida[3]	9	8*	48
T. platycarpa[2]	1	2*	14
V. ambacensis[2]	1	1	9

* Sampling events were not consecutive, they may be spread within the same season or over several seasons.
[1] Tokpa/Ayou, [2] Lema, [3] IITA

Table 7.2. Parasitism of larvae of *M. vitrata* encountered in wild host plants over a period of 2 ½ years (March 1995-August 1997). DAP was indicated when parasitism events in wild hosts happened during cowpea cultivation. L = larvae collected during the respective sampling day in flower material per given volume, par = parasitized larvae, % = percentage parasitism, Paras = parasitoid isolated from parasitized larvae, P = *Phanerotoma leucobasis*, B = *Braunsia kriegeri*. The listed plants are those which at least once revealed parasitism on larvae.

Region	Host plant	Date	Season	DAP	L	par	%	Paras
IITA	*T. candida*	10.05.95	I/95	0	3	0	0.0	
		07.06.95		7	3	0	0.0	
		14.06.95		14	3	0	0.0	
		13.12.95	I/96		9	0	0.0	
		20.12.95			8	0	0.0	
		27.12.95			1	0	0.0	
		03.01.96			2	0	0.0	
		10.01.96			1	0	0.0	
	C. pubescens	27.11.96	II/96		1	0	0.0	
	A. gangetica	27.11.96			1	0	0.0	
Lema	*T. bracteolata*	26.09.95	II/95	14	1	0	0.0	
		03.10.95		21	1	0	0.0	
		10.10.95		28	4	0	0.0	
		17.10.95		35	11	0	0.0	

		24.09.96	II/96	21	11	1	9.1	B
		01.10.96		28	23	3	13.0	1 P, 2 B
		08.10.96		35	42	14	33.3	1 P, 13 B
	T. platycarpa	10.10.95	II/95	28	4	1	25.0	B
		17.10.95		35	4	0	0.0	
		24.09.96	II/96	21	1	0	0.0	
		01.10.96		28	6	0	0.0	
		08.10.96		35	49	12	24.5	1 P, 11 B
		22.10.96		49	1	0	0.0	
	L. sericeus	03.06.97	I/97		2	0	0.0	
	V. ambacensis	17.10.95	II/95	35	1	0	0.0	
		24.10.95		42	8	0	0.0	
	V. reticulata	22.10.96	II/96	49	43	0	0.0	
	D. africanus	29.10.96	II/96		67	10	14.9	P
		12.11.96			4	0	0.0	
Tokpa/	*C. pubescens*	08.01.96	I/96		1	0	0.0	
Ayou		04.11.96	II/96	63	3	0	0.0	
		11.11.96		70	7	0	0.0	
		18.11.96		77	7	0	0.0	
		25.11.96		84	8	0	0.0	
	L. cyanescens	07.07.97	I/97	42	1	1	100.0	P
		14.07.97		49	2	0	0.0	

Table 7.3. Parasitism of larvae of *M. vitrata* encountered in wild host plants over a period of 2 ½ years (March 1995-August 1997) in two regions, Tokpa/Ayou and Lema. L = larvae collected during the respective sampling day in flower material per given volume across seasons, par = parasitized larvae, % = percentage parasitism, P = *Phanerotoma leucobasis*, B = *Braunsia kriegeri*. Total = all larvae of plants in which at least once parasitism occurred including all events in these plants where zero parasitism occurred, Grand total = all larvae ever encountered during the whole period against all larvae being parasitized including all plants where larvae were collected but parasitism never was recorded.

Host plant	**L**	**par**	**%**	**P**	**B**
L. cyanescens[1]	3	1	33.3	1	
T. platycarpa[2]	65	13	19.7	1	12
T. bracteolata[2]	93	18	19.4	2	16
D. africanus[2]	71	10	14.1	10	
Total	**232**	**42**	**18.1**	**14**	**28**
Grand total	**344**	**42**	**12.2**		

[1] Tokpa/Ayou, [2] Lema

Table 7.4. Parasitism of larvae and adults of *M. sjostedti* encountered in wild host plants over a period of 2 ½ years (March 1995-August 1997). DAP was indicated when parasitism events in wild hosts happened during cowpea cultivation. L = larvae collected during the respective sampling day in flower material per given volume, par = parasitized larvae, % = percentage parasitism. The listed plants are those which at least once revealed parasitism in larvae.

Region	Host plant	Date	Season	DAP	L	par	%
IITA	*C. cajan*	07.06.95	I/95	7	92	2	2.2
	C. pubescens	19.02.97	I/97		27	1	3.7
	T. candida	22.03.95	I/95		238	9	3.8
		29.03.95			92	2	2.2
		05.07.95		35	65	3	4.6
		13.12.95	I/96		102	19	18.6
		20.12.95			109	22	20.2
		27.12.95			108	8	7.4
		03.01.96			40	2	5.0
		17.01.96			52	1	1.9
		14.02.96			71	4	5.6
Lema	*C. planchoni*	26.11.96	II/96		50	35	70.0
		10.12.96	I/97		102	10	9.8
	D. africanus	22.10.96	II/96	49	95	6	6.3
		29.10.96		56	126	13	10.3
		05.11.96		63	89	3	3.4
		12.11.96		70	64	8	12.5
	E. griseum	01.10.96	II/96	28	75	8	10.7
		15.10.96		42	105	2	1.9
	E. senegalensis	22.10.96	II/96	49	129	30	23.3
	L. sericeus	03.06.97	I/97	7	31	9	29.0
	P. erinaceus	07.01.97	I/97		149	2	1.3
	T. bracteolata	24.09.96	II/96	21	242	47	19.4
		01.10.96		28	192	14	7.3
		08.10.96		35	493	33	6.7
		15.10.96		42	280	6	2.1
		22.10.96		49	195	2	1.0
	T. platycarpa	24.09.96	II/96	21	23	7	30.4
		01.10.96		28	154	11	7.1
		08.10.96		35	493	32	6.5
		15.10.96		42	194	1	0.5
		22.10.96		49	122	1	0.8

Tokpa/ Ayou	*C. cajan*	28.10.96	II/96	56	84	1	1.2
	C. pubescens	11.12.95	I/96		63	1	1.6
		18.12.95			76	12	15.8
		08.01.96			35	2.5	7.1
		15.01.96			80	2	2.5
		18.11.96	II/96	77	116	1	0.9
		30.12.96	I/97		44	2	4.5
		06.01.97			102	11	10.8
		27.01.97			85	1	1.2
	L. cyanescens	30.06.97	I/97	35	29	2	6.9
		07.07.97		42	142	6	4.2

Table 7.5. Parasitism of larvae and adults of *M. sjostedti* encountered in wild host plants over a period of 2 ½ years (March 1995-August 1997) in three regions, Tokpa/Ayou, Lema and IITA. L = larvae collected during the respective sampling day in flower material per given volume across seasons, par = parasitized larvae, % = percentage parasitism. Total = all larvae of plants in which at least once parasitism occurred including all events in these plants where zero parasitism occurred, Grand total = all larvae ever encountered during the whole period against all larvae being parasitized including all plants where larvae were collected but parasitism never was recorded.

Region	**Host plant**	**L**	**par**	**%**
IITA	*T. candida*	2,270	70	3.1
	C. cajan	412	2	0.5
	C. pubescens	592	1	0.2
	Total	**3,274**	**73**	**2.2**
Lema	*L. sericeus*	31	9	29.0
	C. planchoni	235	45	19.1
	E. senegalensis	558	81	14.5
	D. africanus	374	30	8.0
	T. bracteolata	1,750	102	5.8
	E. griseum	199	10	5.0
	T. platycarpa	1,142	52	4.6
	P. erinaceus	149	2	1.3
	Total	**4,438**	**331**	**7.5**
ToAyou	*L. cyanescens*	231	8	3.5
	C. pubescens	2,102	35	1.7
	C. cajan	282	1	0.4
	Total	**2,615**	**44**	**1.7**
	Grand total	**10,521**	**448**	**4.3**

Fig. 2.1. Soil humidity in 3 regions, Tokpa/Ayou, Lema, IITA, per season, sampling interval DAP 0-70: amount of water loss per sample (arcsine √p transformed) over time (DAP) (biweekly sampling interval); season I/96 = 0-10 cm depth, seasons II/96 and I/97 = 0-60 cm depth; trend between regions: IITA (I), Tokpa/Ayou (ToAy), Lema (Le), n (number of observations) = 486, $F_{(20,346)}$ = 25.7, $P << 0.01$.

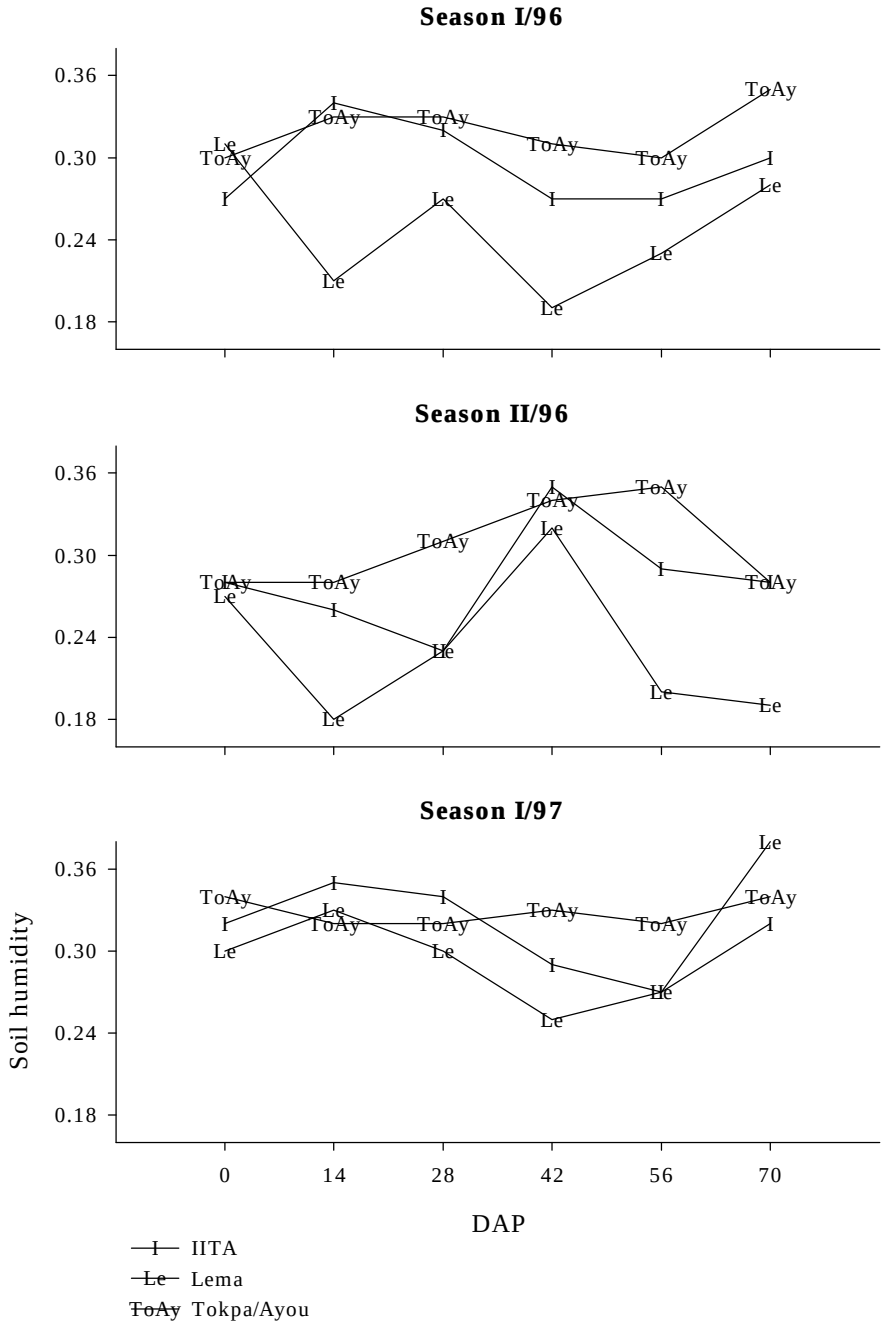


Fig. 2.2. Tokpa/Ayou, seasons I/96-I/97, sampling interval DAP 0-70: a) Soil humidity, amount of water loss per sample (arcsine √p transformed) over time (DAP) (biweekly sampling interval); season I/96 = 0-10 cm depth, seasons II/96 and I/97 = 0-60 cm depth; trend between seasons: season I/96 (3), season II/96 (4), season I/97 (5), n = 324, $F_{(10,230)}$ = 26.9, P << 0.01; b) Precipitation in mm (sum of preceding week).

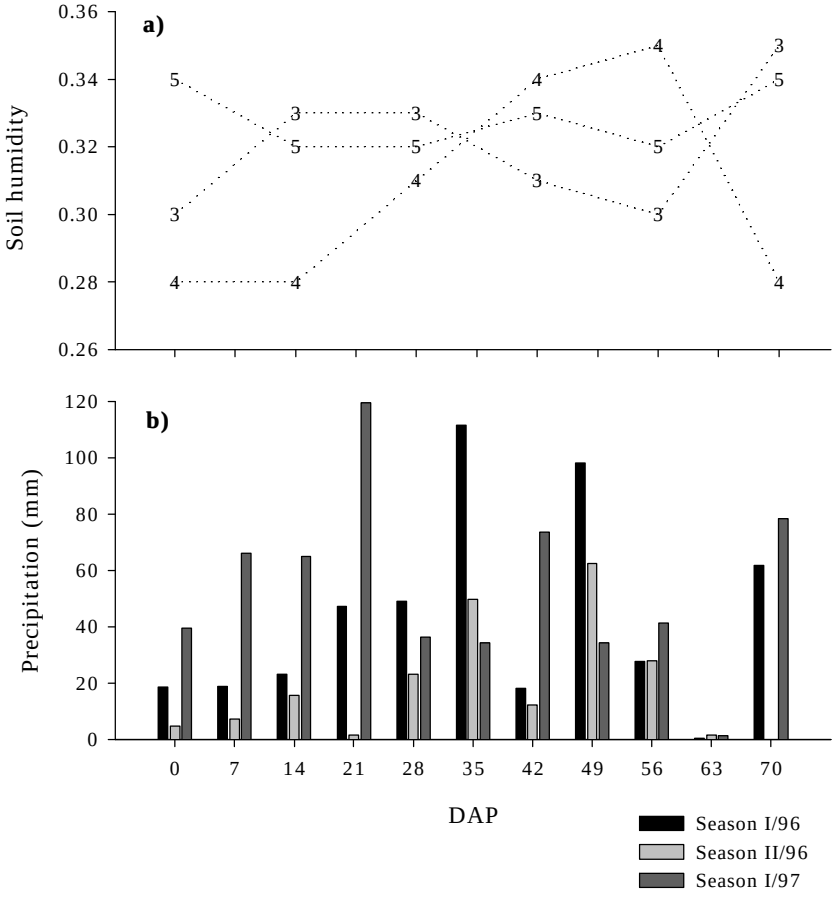


Fig. 2.3. Lema, seasons I/96-I/97, sampling interval DAP 0-70: soil humidity as amount of water loss per sample (arcsine √p transformed) over time (DAP) (biweekly sampling interval); season 3 (I/96) = 0-10 cm depth, seasons 4 (II/96) and 5 (I/97) = 0-60 cm depth: a) Trend (across seasons) with (1)/ without (0) NPK, n = 324, $F_{(5,230)} = 3.0^{[c]}$, $P < 0.01$; b) Trend between seasons, n = 324, $F_{(10,230)} = 84.1$, $P << 0.01$; c) Precipitation in mm (sum of preceding week).

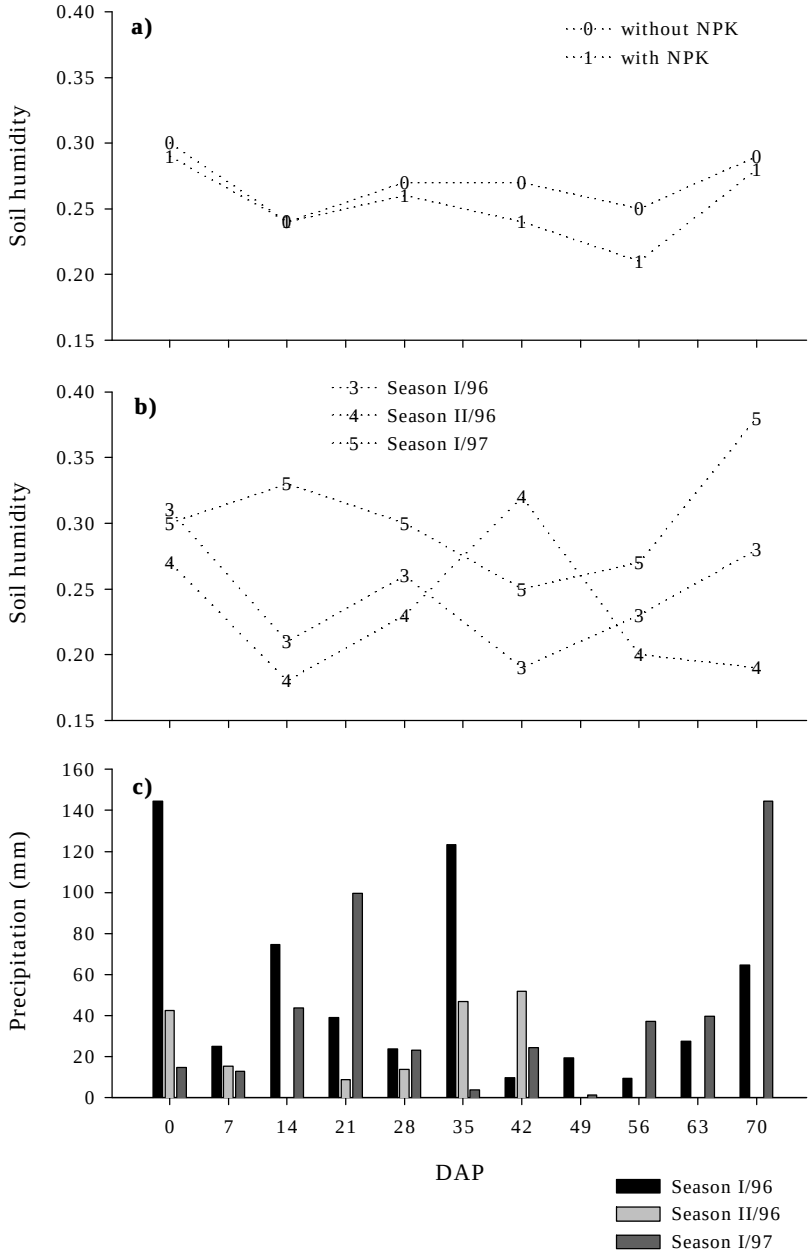


Fig. 2.4. IITA, seasons I/96-I/97, sampling interval DAP 0-70: a) Soil humidity as amount of water loss per sample (arcsine √p transformed) over time (DAP) (biweekly sampling interval); season 3 (I/96) = 0-10 cm depth, seasons 4 (II/96) and 5 (I/97) = 0-60 cm depth; trend between seasons, n = 216, $F_{(10,138)} = 61.4$, $P << 0.01$; b) Precipitation in mm (sum of preceding week).

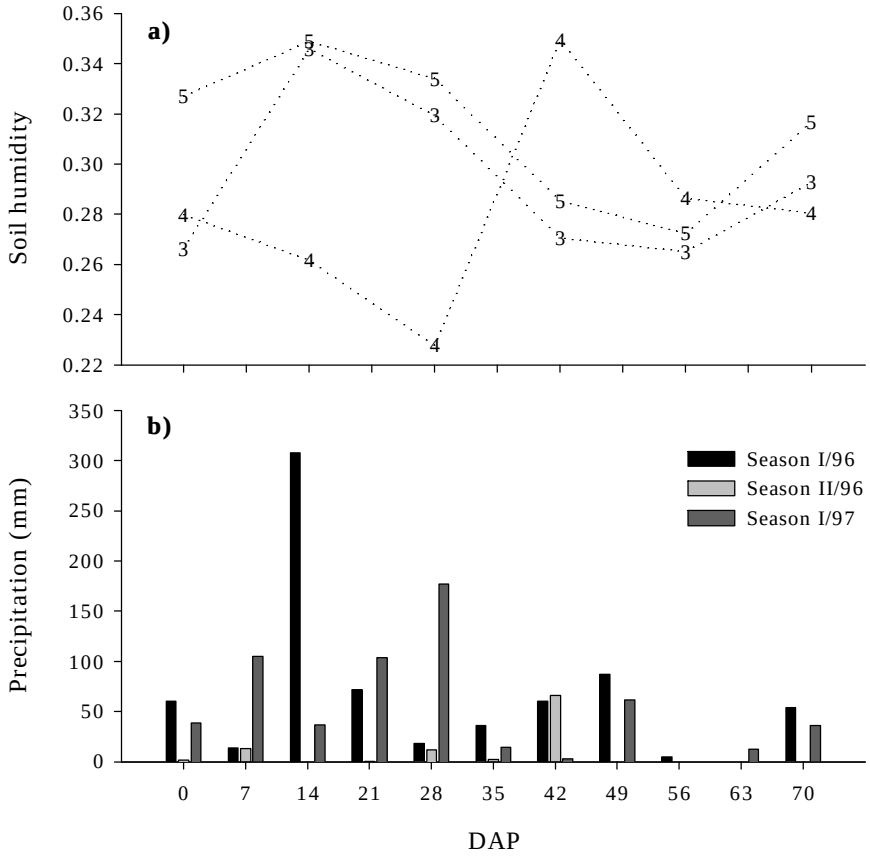


Fig. 2.5. Tokpa/Ayou, season I/95, sampling interval DAP 21-70: a) Precipitation (ð) (sum of preceding week in mm); b)-d) Plant phenology (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Nodes per plant (⁻), n = 144, $P \geq 0.05$; c) Flowers per plant (⁻), n = 90, $P \geq 0.05$; flower index (¨) (flowers per nodes per plant) (arcsine √p transformed), n = 90, $P \geq 0.05$; d) Pods per plant, n = 90, $P \geq 0.05$.

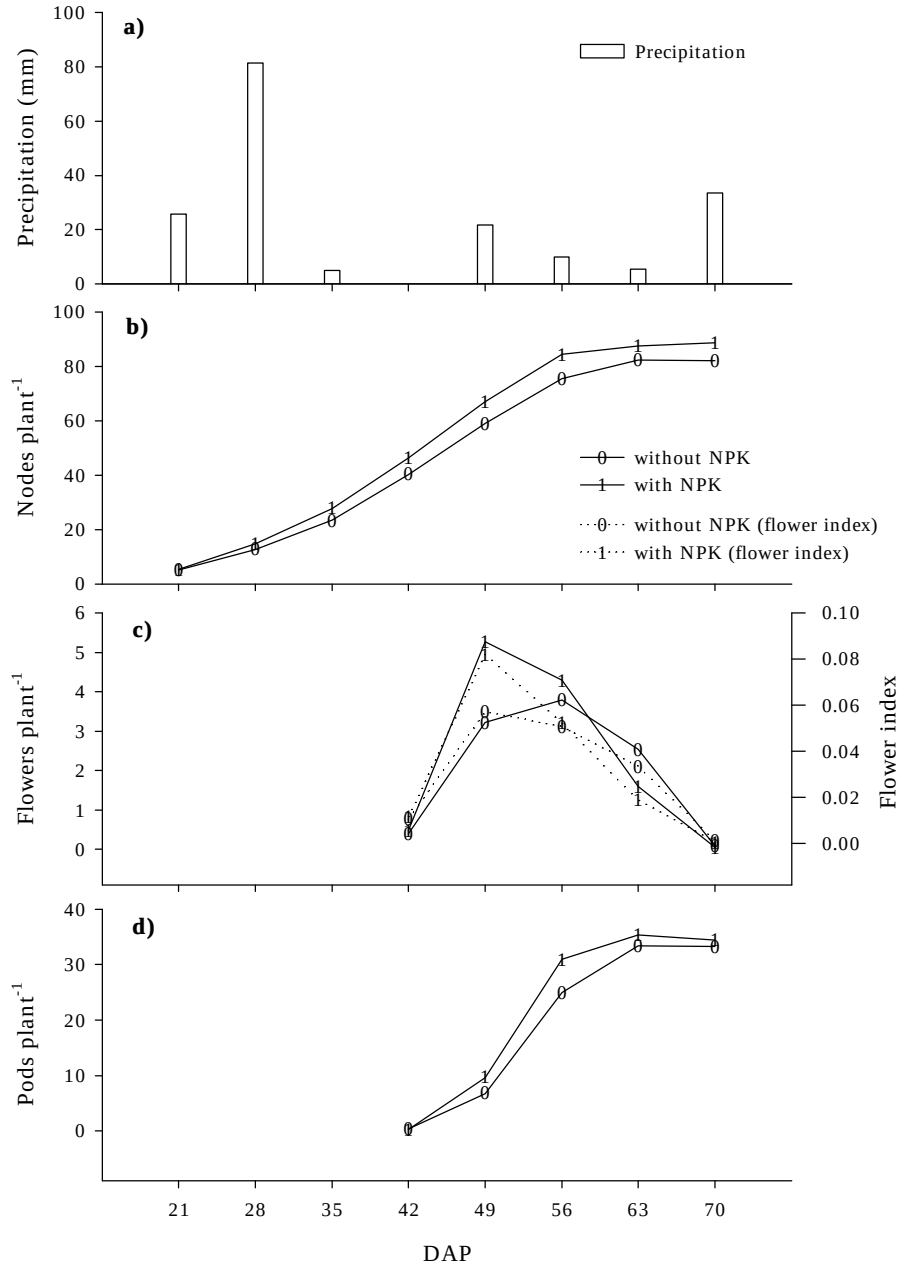


Fig. 2.6. Tokpa/Ayou, season II/95, sampling interval DAP 35-70: a) Precipitation (ð) (sum of preceding week in mm); b)-d) Plant phenology (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Nodes per plant (⁻), trend on NPK, n = 108, $F_{(5,70)} = 5.6$, $P < 0.01$; c) Flowers per plant (⁻), n = 90, $P \geq 0.05$, flower index (¨) (flowers per nodes per plant) (arcsine √p transformed), NPK main effect, n = 90, $F_{(1,58)} = 5.6$, $P < 0.05$; d) Pods per plant (⁻), n = 90, $P \geq 0.05$.

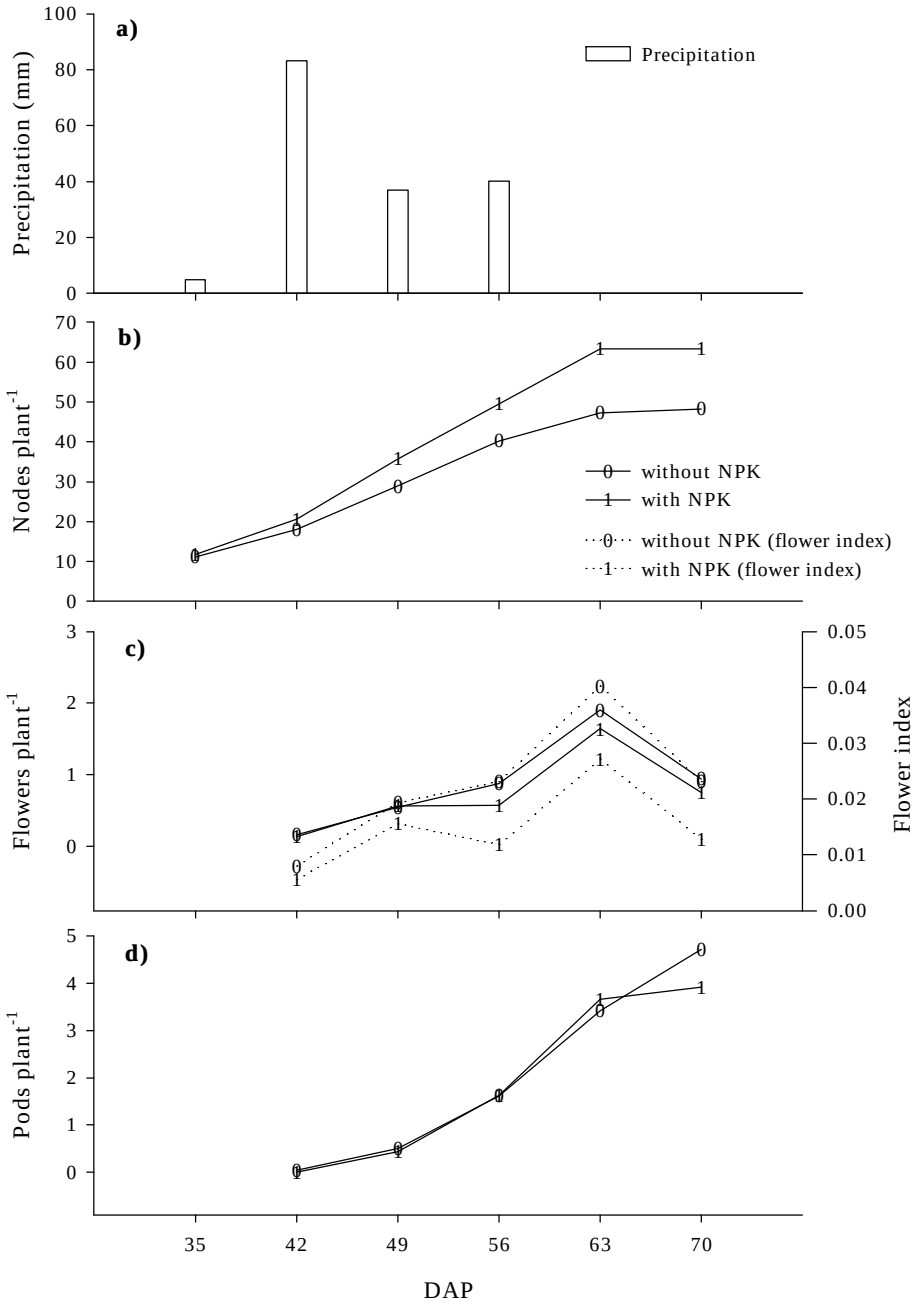


Fig. 2.7. Tokpa/Ayou, season I/96, sampling interval DAP 35-70: effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): a) Soil humidity (biweekly sampling interval; arcsine √p transformed), NPK main effect, n = 108, $F_{(1,70)} = 7.7$, $P < 0.01$; precipitation (ð) (sum of preceding week in mm); b) Nodes per plant (⁻) (detransformed), trend on NPK, n = 108, $F_{(5,70)} = 5.1$, $P < 0.01$; c) Flowers per plant (⁻) (detransformed), n = 90, $P \geq 0.05$; flower index (···) (flowers per nodes per plant) (arcsine √p transformed), n = 72, $P \geq 0.05$; d) Pods per plant (⁻) (detransformed), NPK main effect, n = 90, $F_{(1,58)} = 10.0$, $P < 0.01$.

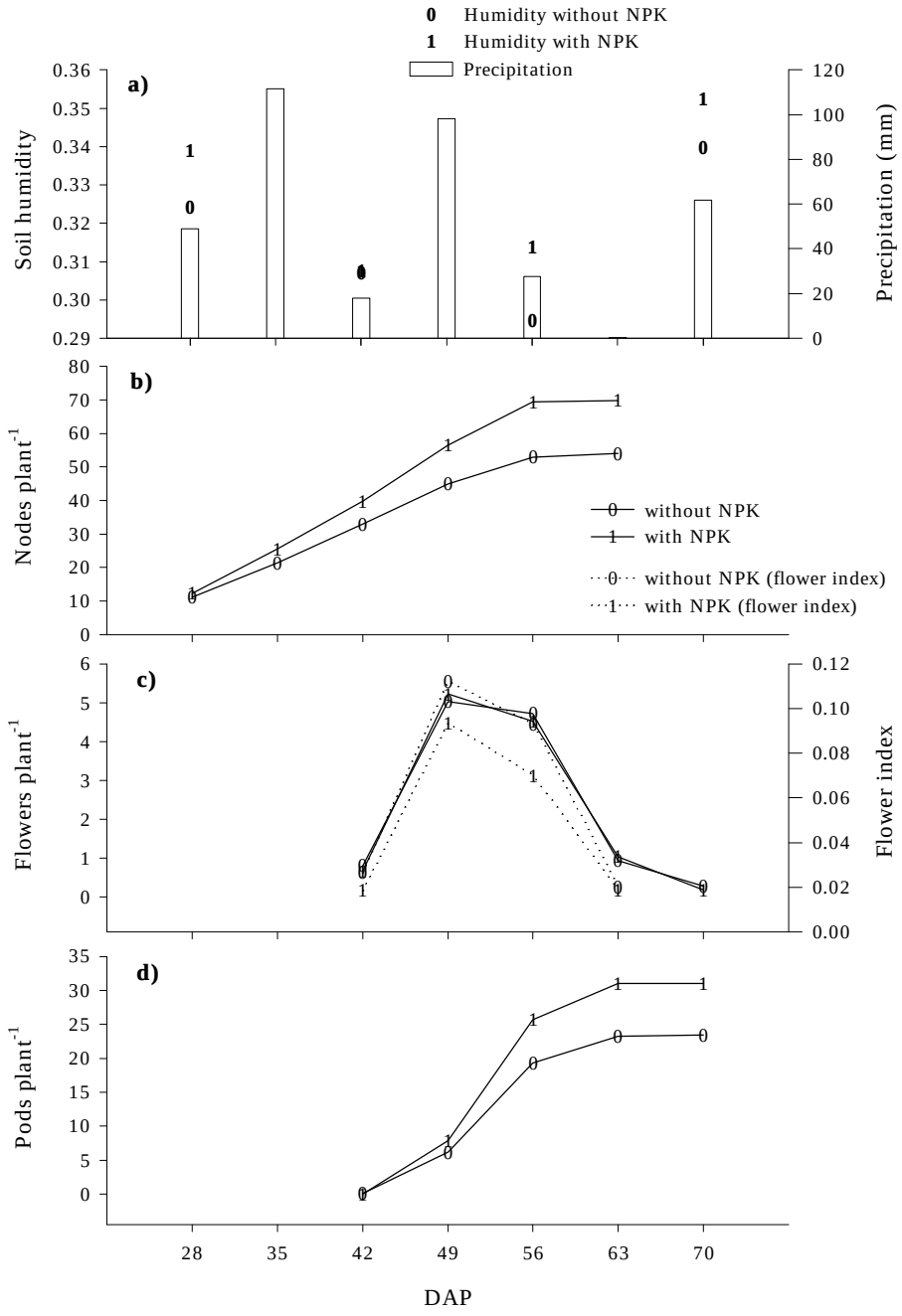


Fig. 2.8. Tokpa/Ayou, season II/96, sampling interval DAP 42-70: effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): a) Soil humidity (biweekly sampling interval; arcsine √p transformed), n = 108, $P \geq 0.05$; precipitation (ð) (sum of preceding week in mm); b) Nodes per plant (⁻) (detransformed), trend on NPK, n = 54, $F_{(2,34)} = 15.2$, $P << 0.01$; c) Flowers per plant (⁻) (detransformed), n = 72, $P \geq 0.05$; flower index (¨) (flowers per nodes per plant) (arcsine √p transformed), n = 36, $P \geq 0.05$; d) Pods per plant (⁻) (detransformed), trend on NPK, n = 72, $F_{(3,46)} = 4.6$, $P < 0.01$.

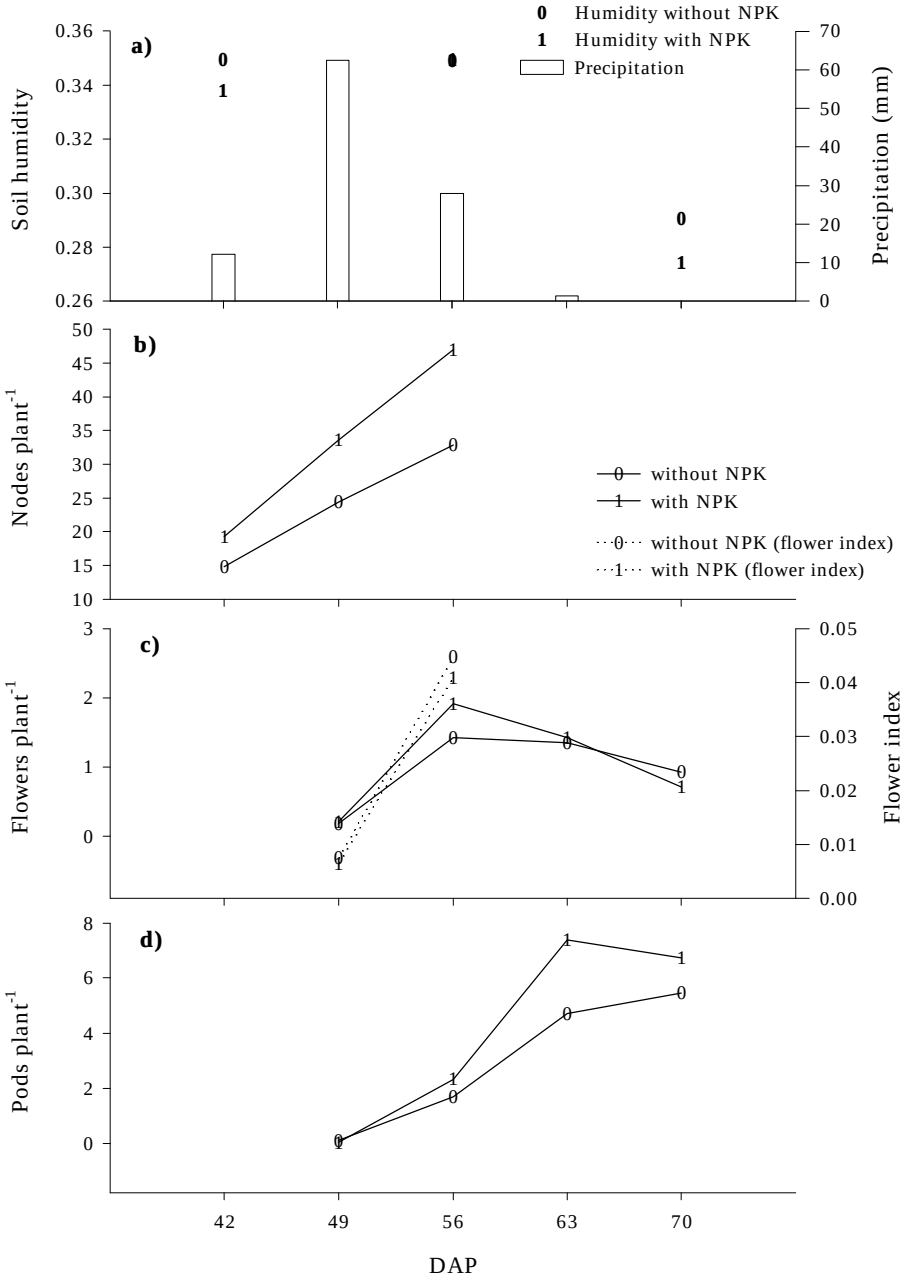


Fig. 2.9. Tokpa/Ayou, season I/97, sampling interval DAP 42-84: effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): a) Soil humidity (•) (biweekly sampling interval; arcsine √p transformed), n = 108, $P \geq 0.05$; precipitation (ð) (sum of preceding week in mm); b) Nodes per plant (⁻) (detransformed), trend on NPK, n = 90, $F_{(4,58)} = 2.8^{[l]}$, $P < 0.05$, trend on mulch, n = 90, $F_{(8,58)} = 2.9$, $P < 0.01$; c) Flowers per plant (⁻) (detransformed), trend on NPK, n = 126, $F_{(6,82)} = 5.5$, $P << 0.01$; flower index (···) (flowers per nodes per plant) (arcsine √p transformed), trend on NPK, n = 90, $F_{(4,58)} = 17.4^{[q]}$, $P << 0.01$; d) Pods per plant (⁻) (detransformed), mulch main effect, n = 90, $F_{(2,58)} = 4.3$, $P < 0.05$.

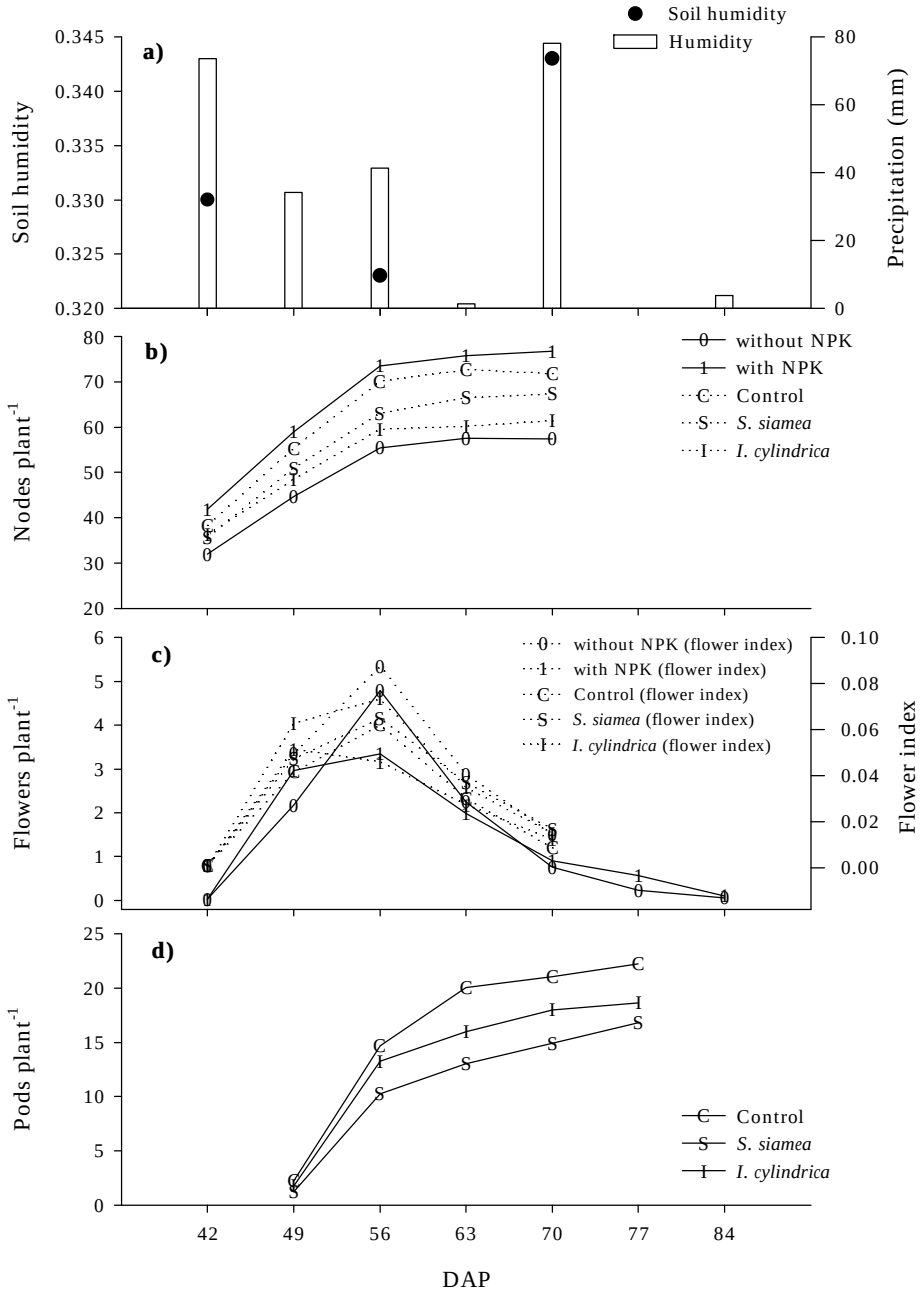


Fig. 2.10. Lema, season I/95, sampling interval DAP 21-70: a) Precipitation (ð) (sum of preceding week in mm); b)-d) Plant phenology (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Nodes per plant (⁻), trend on NPK, n = 144, $F_{(7,94)} = 5.6$, $P << 0.01$; c) Flowers per plant (⁻), n = 54, $P \geq 0.05$; flower index (···) (flowers per nodes per plant) (arcsine √p transformed), n = 90, $P \geq 0.05$; d) Pods per plant (⁻), n = 90, $P \geq 0.05$.

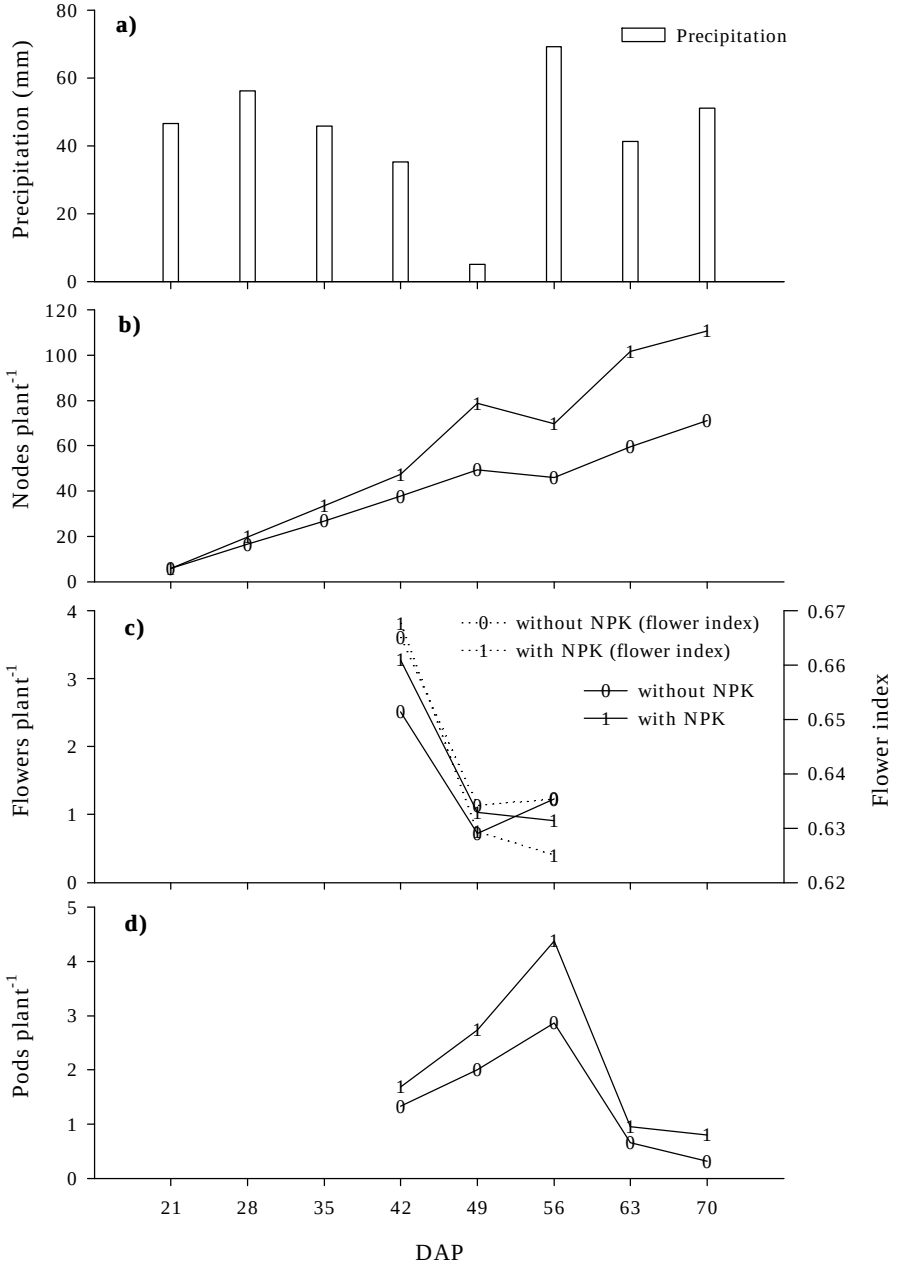


Fig. 2.11. Lema, season II/95, sampling interval DAP 35-70: a) Precipitation (ð) (sum of preceding week in mm); b)-d) Plant phenology (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Nodes per plant (⁻), trend on NPK, n = 108, $F_{(5,70)} = 11.8^{[l]}$, $P << 0.01$; c) Flowers per plant (⁻), n = 72, $P \geq 0.05$; flower index (···) (flowers per nodes per plant) (arcsine √p transformed), trend on NPK, n = 90, $F_{(4,58)} = 2.9^{[q]}$, $P < 0.05$; d) Pods per plant (⁻), trend on NPK, n = 72, $F_{(3,46)} = 4.3^{[l]}$, $P < 0.01$.

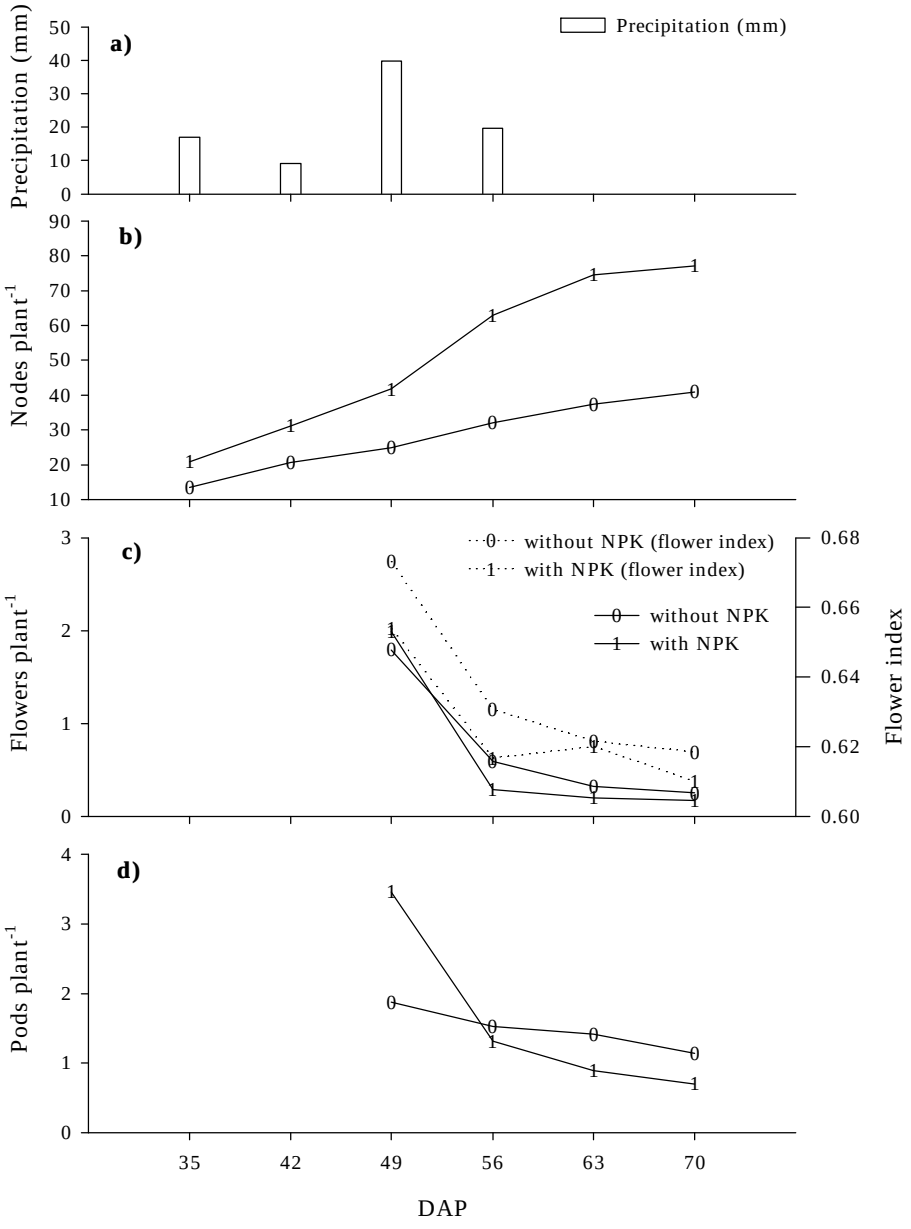


Fig. 2.12. Lema, season I/96, sampling interval DAP 28-70: effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): a) Soil humidity (biweekly sampling interval; arcsine √p transformed), n = 108, $P \geq 0.05$; precipitation (ð) (sum of preceding week in mm); b) Nodes per plant (⁻) (detransformed), trend on NPK, n = 108, $F_{(5,70)} = 31.0^{[l]}$, $P << 0.01$; c) Flowers per plant (⁻) (detransformed), trend on NPK, n = 108, $F_{(5,70)} = 3.7^{[l]}$, $P < 0.01$; flower index (¨) (flowers per nodes per plant) (arcsine √p transformed), trend on NPK, n = 72, $F_{(3,46)} = 3.9^{[q]}$, $P < 0.05$; d) Pods per plant (⁻) (detransformed), trend on NPK, n = 90, $F_{(4,58)} = 5.5^{[q]}$, $P < 0.01$.

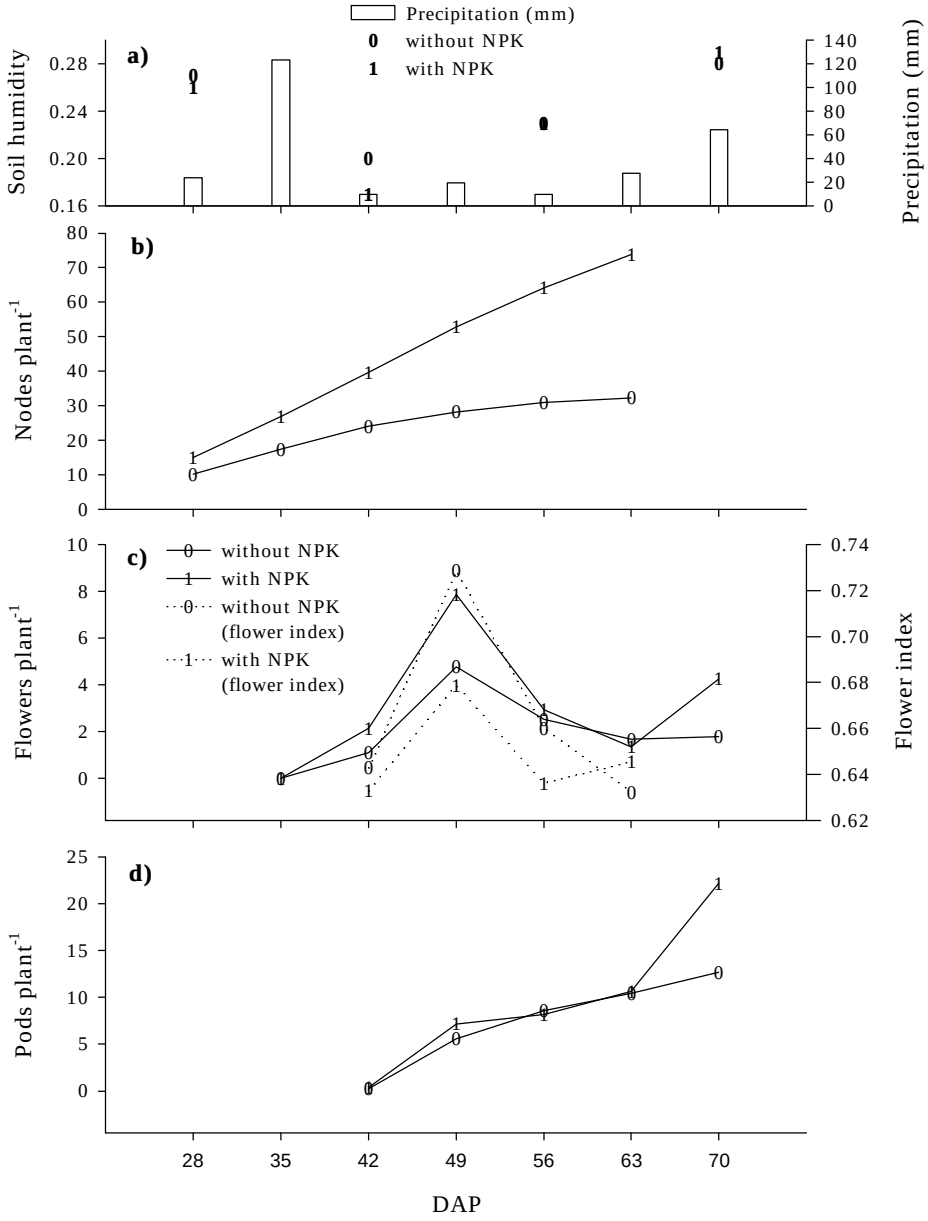


Fig. 2.13. Lema, season II/96, sampling interval DAP 35-70: effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): a) Soil humidity (•) (bi-weekly sampling interval; arcsine √p transformed), n = 108, $P \geq 0.05$; precipitation (ð) (sum of preceding week in mm); b) Nodes per plant (⁻) (detransformed), trend on NPK, n = 72, $F_{(3,46)} = 3.8^{[l]}$, $P < 0.05$; c) Flowers per plant (⁻) (detransformed), trend on NPK, n = 108, $F_{(5,70)} = 4.5^{[q]}$, $P < 0.01$, trend on mulch, n = 90, $F_{(8,58)} = 2.9$, $P < 0.01$; d) Flower index (¨) (flowers per nodes per plant) (arcsine √p transformed), trend on NPK, n = 54, $F_{(2,34)} = 5.0^{[l]}$, $P < 0.05$, trend on mulch, n = 54, $P \geq 0.05$; e) Pods per plant (⁻) (detransformed), trend on NPK, n = 90, $F_{(4,58)} = 8.5^{[q]}$, $P << 0.01$.

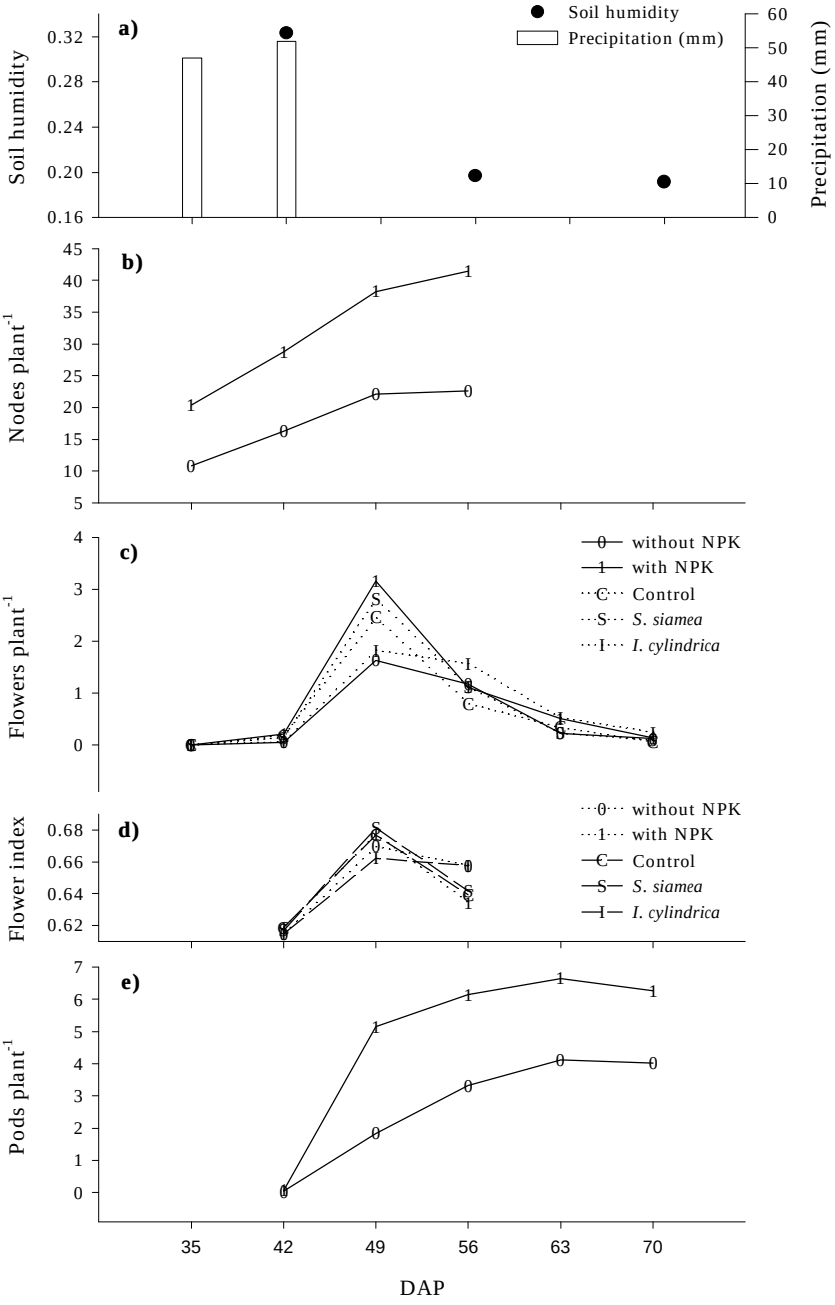


Fig. 2.14. Lema, season I/97, sampling interval DAP 42-91: effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): a) Soil humidity (biweekly sampling interval; arcsine √p transformed), trend on NPK, n = 108, $F_{(1,70)} = 6.3$, $P < 0.05$; precipitation (ð) (sum of preceding week in mm); b) Nodes per plant (⁻) (detransformed), trend on NPK, n = 90, $F_{(4,58)} = 19.3^{[I]}$, $P << 0.01$, trend on mulch, n = 90, $F_{(8,58)} = 2.6$, $P < 0.05$; c) Flowers per plant (⁻) (detransformed), NPK main effect, n = 144, $F_{(1,94)} = 5.0$, $P < 0.05$; d) Flower index (¨) (flowers per nodes per plant) (arcsine √p transformed), NPK main effect, n = 90, $F_{(1,58)} = 14.5$, $P < 0.01$, mulch main effect, n = 90, $F_{(2,58)} = 3.8$, $P < 0.05$. e) Pods per plant (⁻) (detransformed), NPK main effect, n = 108, $F_{(1,70)} = 6.7$, $P < 0.05$, mulch main effect, n = 108, $F_{(2,70)} = 6.6$, $P < 0.01$.

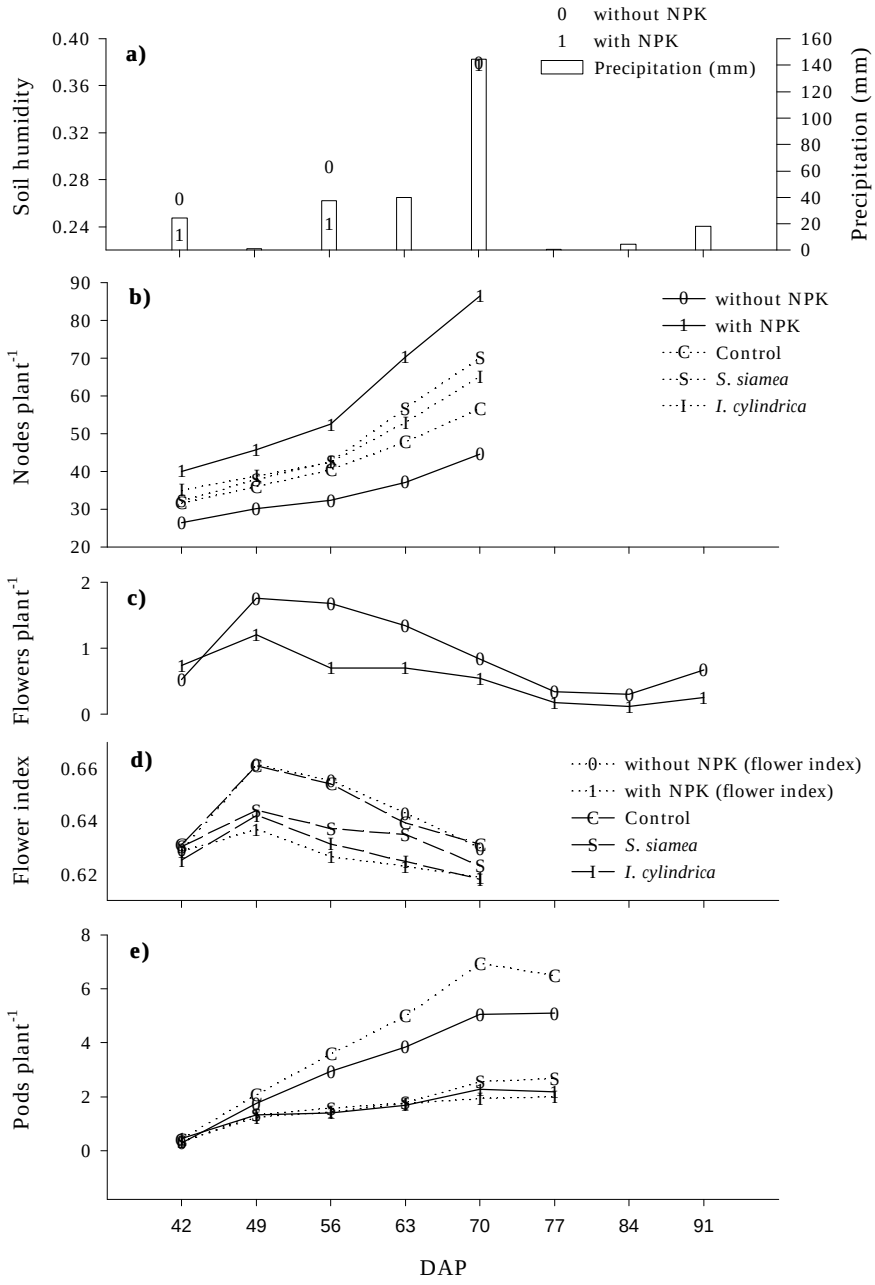


Fig. 2.15. IITA, season I/95, sampling interval DAP 21-70: a) Precipitation (ð) (sum of preceding week in mm); b)-e) Plant phenology (detransformed data): effects on mulch, control (C), *S. siamea* (S), *I. cylindrica* (I) and *A. indica* (A): b) Nodes per plant (⁻), main effect, n = 96, $F_{(3,62)} = 9.4$, $P << 0.01$; c) Flowers per plant (⁻), n = 60, $P \geq 0.05$; d) Flower index (¨) (flowers per nodes per plant) (arcsine √p transformed), n = 60, $P \geq 0.05$; e) Pods per plant (⁻), main effect, n = 60, $F_{(3,38)} = 6.6$, $P < 0.01$.

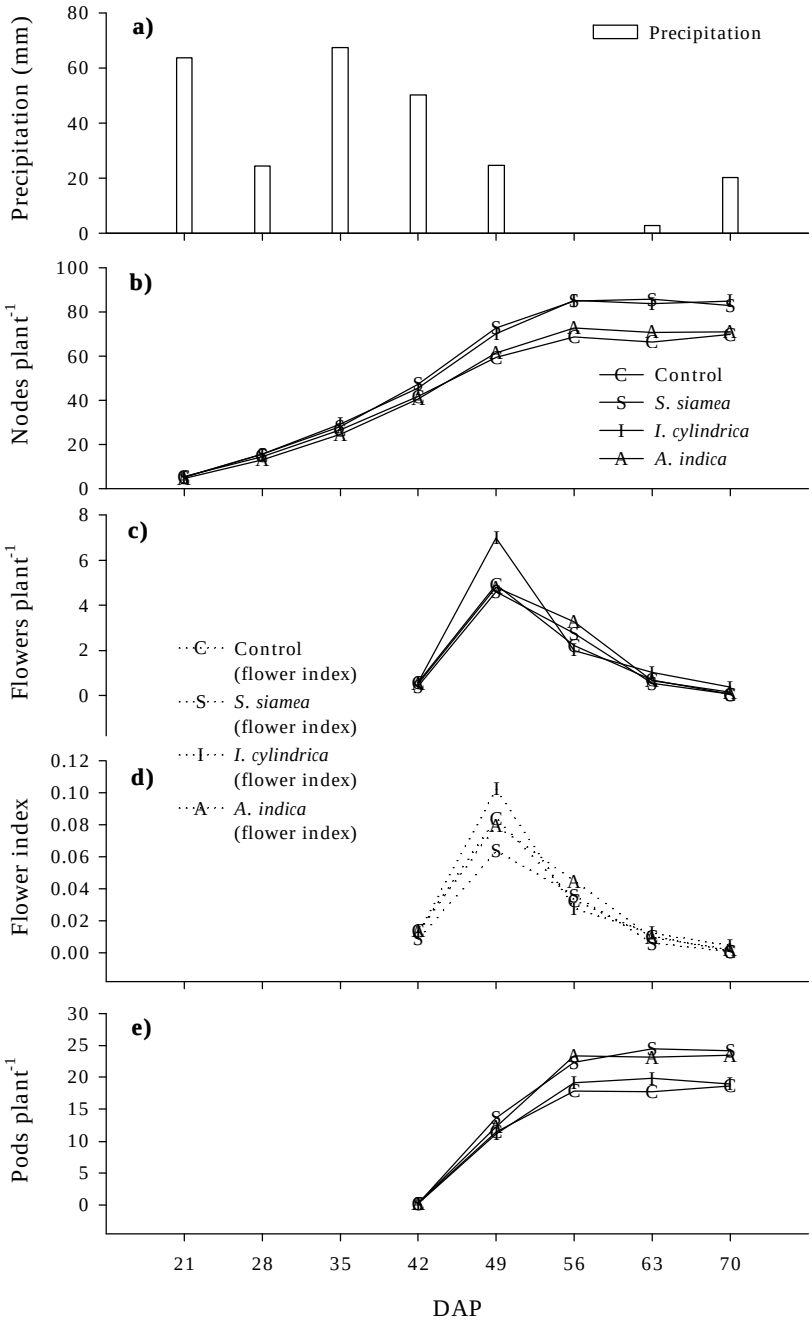


Fig. 2.16. IITA, season II/95, sampling interval DAP 35-70: a) Precipitation (ð) (sum of preceding week in mm); b)-e) Plant phenology (detransformed data): effects on mulch, control (C), *S. siamea* (S), *I. cylindrica* (I) and *A. indica* (A): b) Nodes per plant (⁻), n = 72, $P \geq 0.05$; c) Flowers per plant (⁻), n = 60, $P \geq 0.05$; d) Flower index (¨) (flowers per nodes per plant) (arcsine √p transformed), n = 60, $P \geq 0.05$; e) Pods per plant (⁻), n = 60, $P \geq 0.05$.

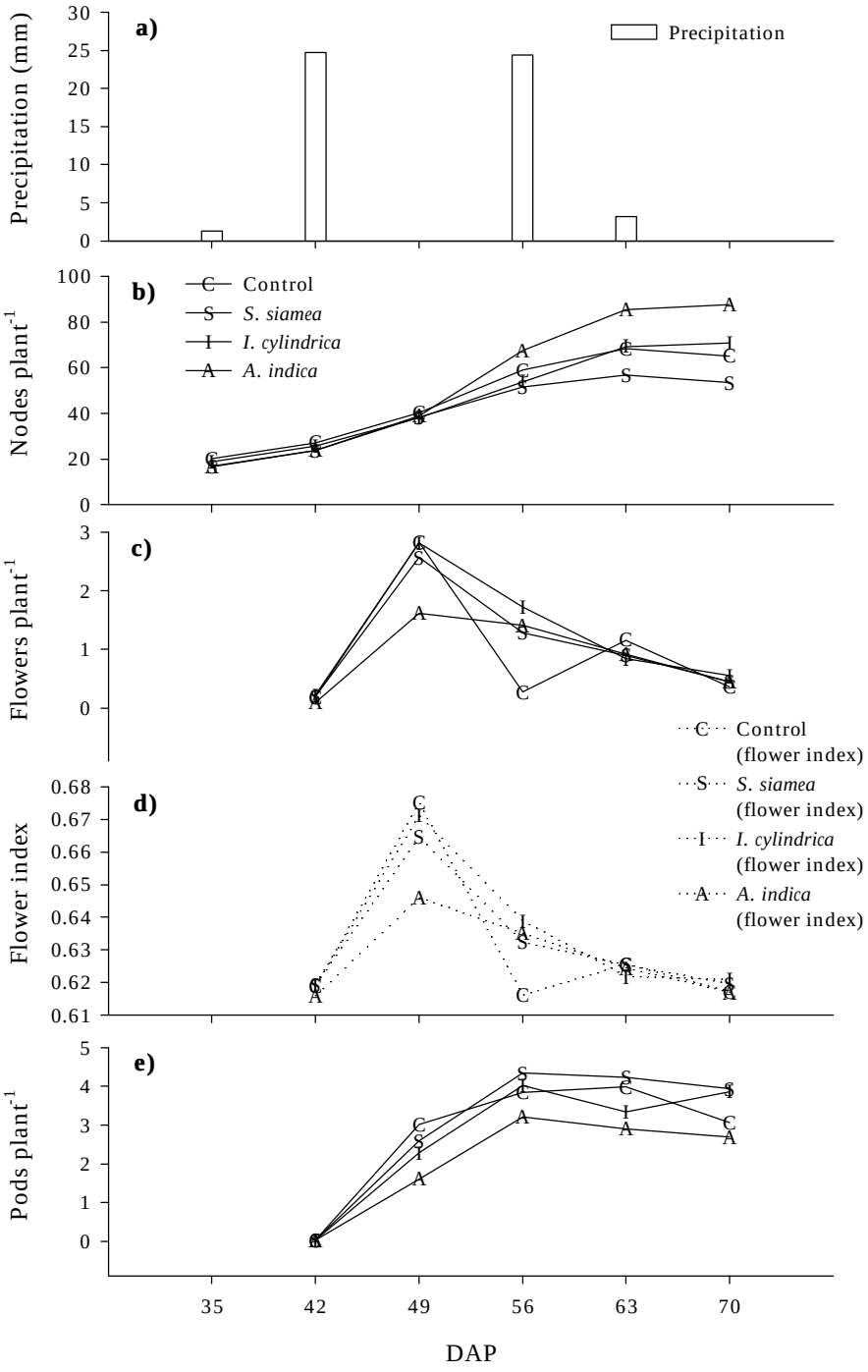


Fig. 2.17. IITA, season I/96, sampling interval DAP 21-70: effects on mulch, control (C), *S. siamea* (S), *I. cylindrica* (I) and *A. indica* (A): a) Soil humidity (biweekly sampling interval; arcsine √p transformed), trend, n = 72, $F_{(3,46)} = 3.8$, $P < 0.05$; precipitation (ð) (sum of preceding week in mm); b) Nodes per plant (⁻) (detransformed), main effect, n = 84, $F_{(3,54)} = 3.2$, $P < 0.05$; c) Flowers per plant (⁻) (detransformed), n = 60, $P \geq 0.05$; d) Flower index (¨) (flowers per nodes per plant) (arcsine √p transformed), trend, n = 48, $F_{(9,30)} = 2.8^{[q]}$, $P < 0.05$; e) Pods per plant (⁻) (detransformed), main effect, n = 48, $F_{(3,30)} = 7.3$, $P < 0.01$.

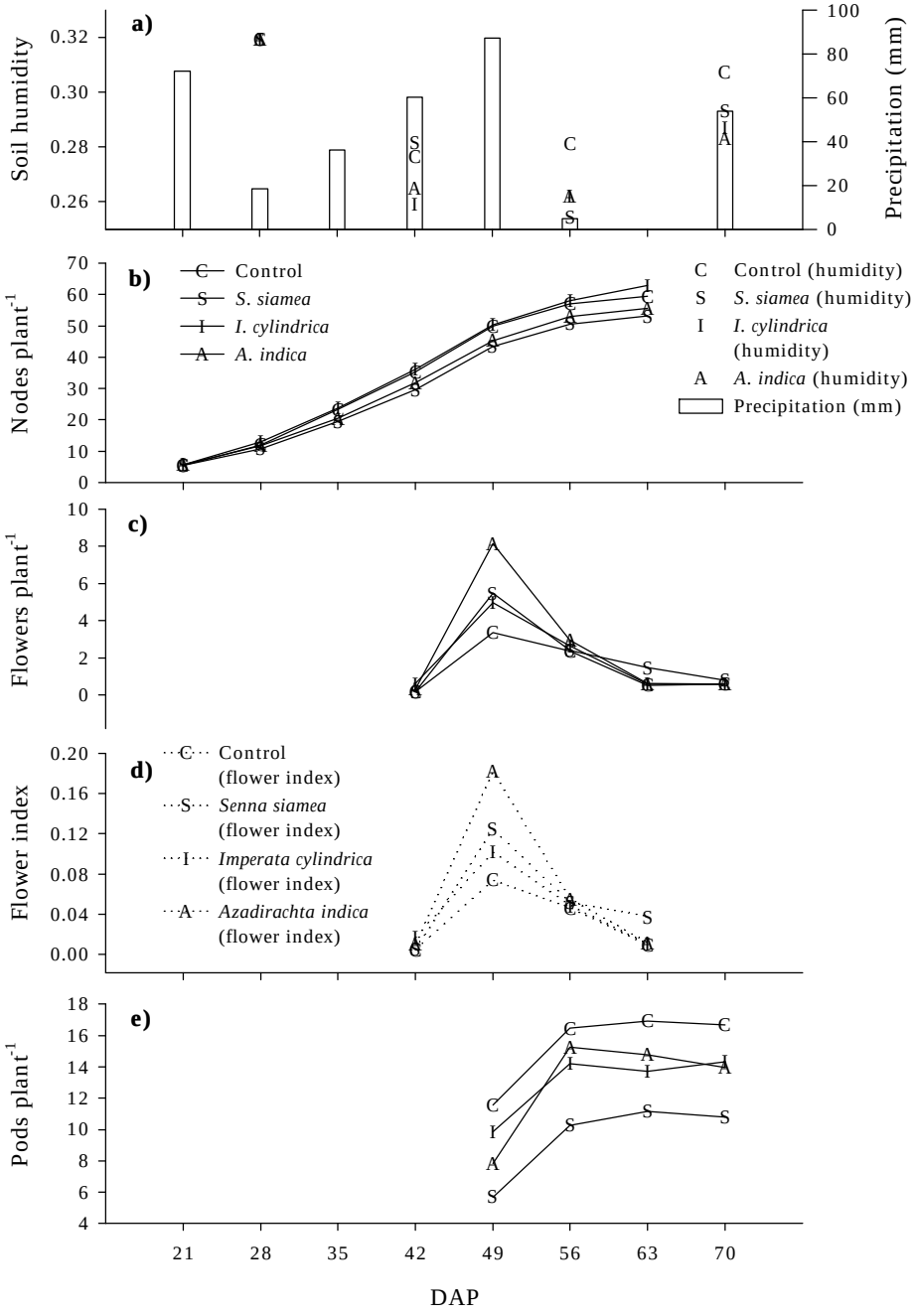


Fig. 2.18. IITA, season II/96, sampling interval DAP 35-70: effects on mulch, control (C), *S. siamea* (S), *I. cylindrica* (I) and *A. indica* (A): a) Soil humidity (•) (biweekly sampling interval; arcsine √p transformed), n = 72, $P \geq 0.05$; precipitation (ð) (sum of preceding week in mm); b) Nodes per plant (⁻) (detransformed), n = 48, $P \geq 0.05$; c) Flowers per plant (⁻) (detransformed), n = 48, $P \geq 0.05$; d) Flower index (¨) (flowers per nodes per plant) (arcsine √p transformed), n = 36, $P \geq 0.05$; e) Pods per plant (⁻) (detransformed), main effect, n = 36, $F_{(3,30)} = 10.5$, $P << 0.01$.

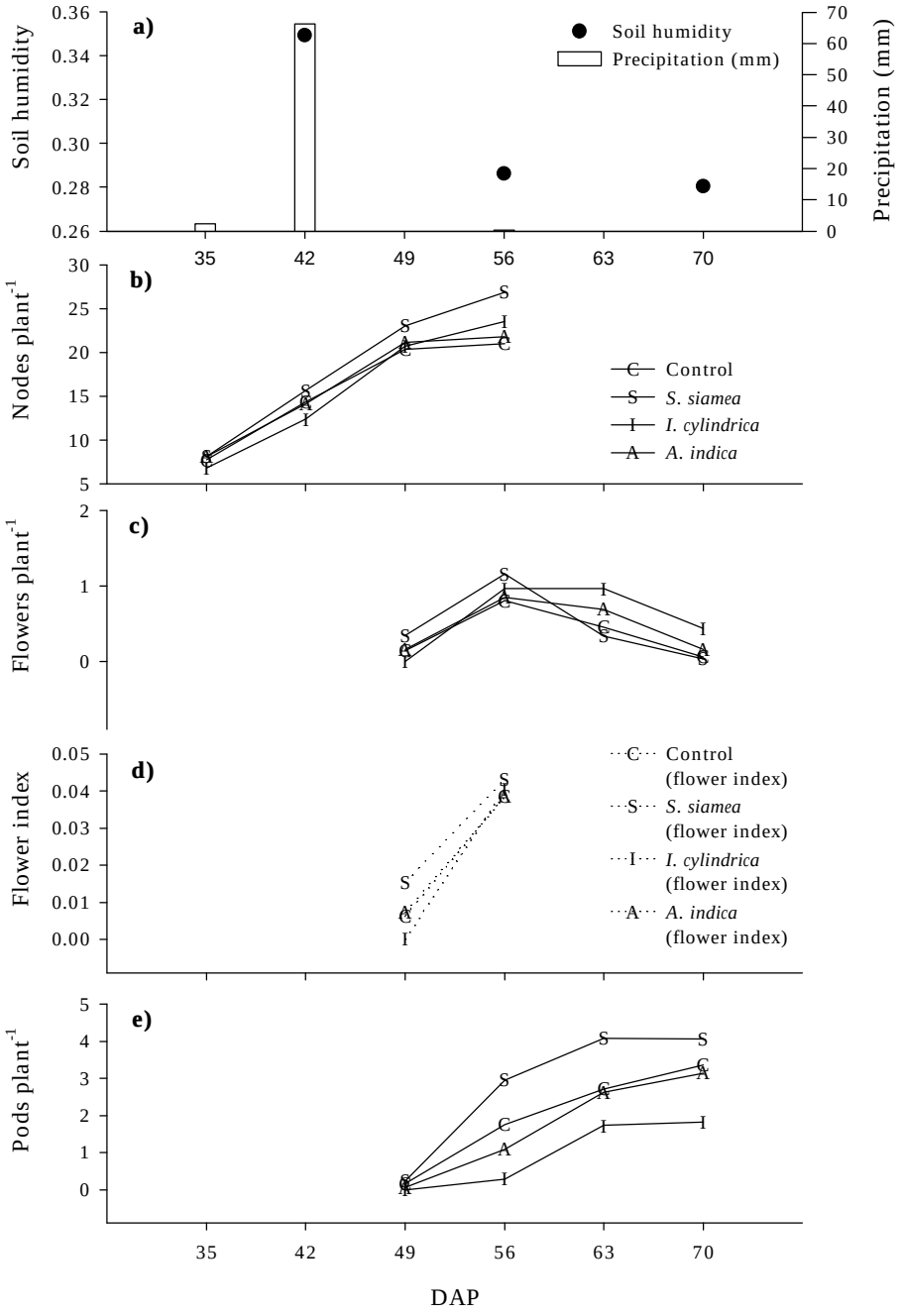


Fig. 2.19. IITA, season I/97, sampling interval DAP 42-77: effects on mulch, control (C), *S. siamea* (S), *I. cylindrica* (I) and *A. indica* (A): a) Soil humidity (•) (biweekly sampling interval; arcsine √p transformed), n = 72, $P \geq 0.05$; precipitation (ð) (sum of preceding week in mm); b) Nodes per plant (⁻) (detransformed), main effect, n = 60, $F_{(3,38)} = 11.9$, $P << 0.01$; c) Flowers per plant (⁻) (detransformed), trend, n = 72, $F_{(15,46)} = 2.1$, $P < 0.05$; d) Flower index (¨) (flowers per nodes per plant) (arcsine √p transformed), n = 60, $P \geq 0.05$; e) Pods per plant (⁻) (detransformed), main effect, n = 72, $F_{(3,46)} = 22.4$, $P << 0.01$.

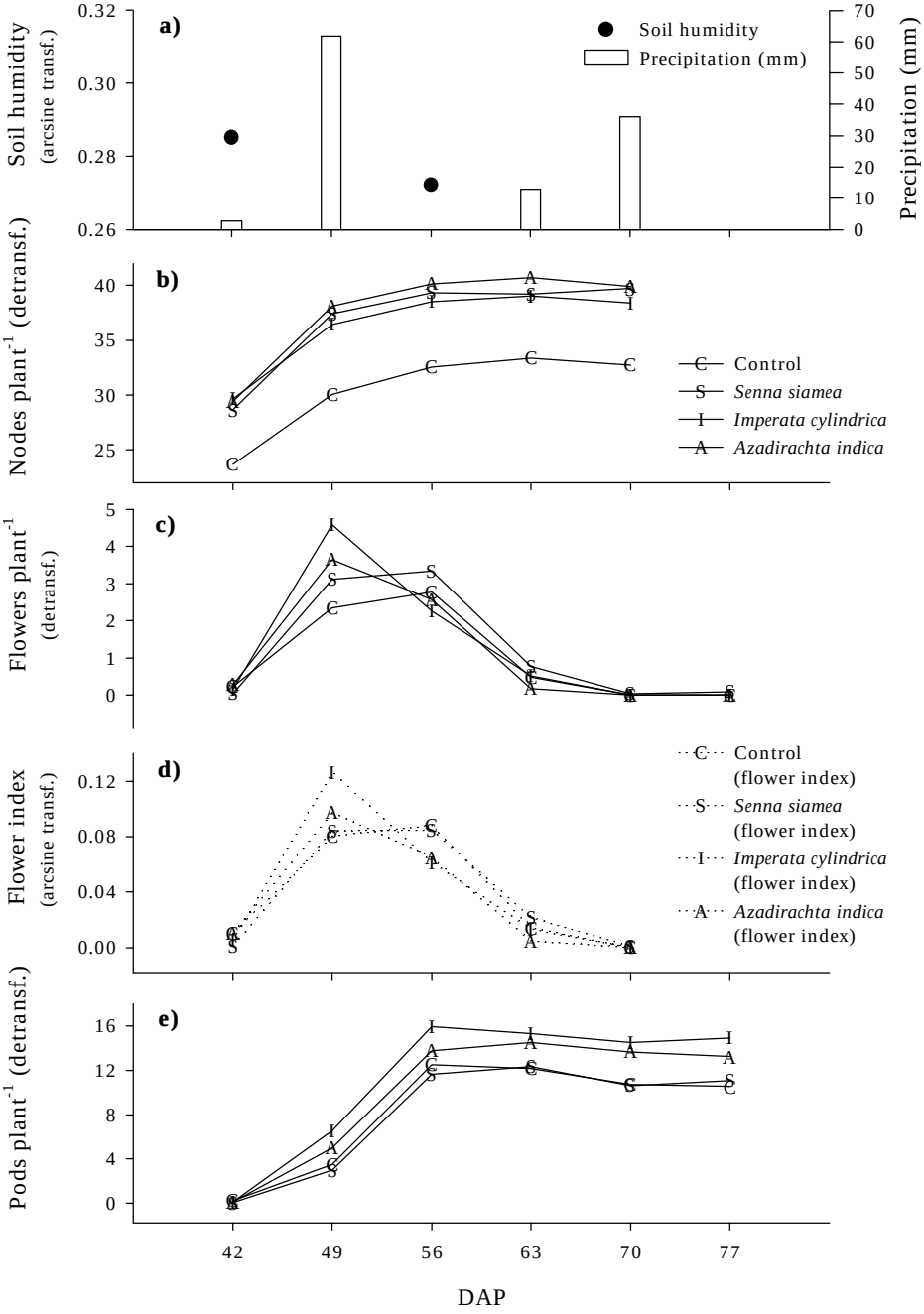


Fig. 3.1. Tokpa/Ayou, season I/95, sampling interval DAP 49-70: a) Precipitation (ð) (sum of preceding week in mm) and mean temperature (¨) (weekly mean of preceding week in °C); b)-d) Population dynamics as abundance (⁻) and density index (¨) (number of insects per flower, actual counts on phenology) (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Larvae of *M. vitrata* per 20 flowers, n = 66, $P \geq 0.05$; density index, n = 53, $P \geq 0.05$; c) Larvae of *M. sjostedti* per flower, trend on NPK, n = 66, $F_{(3,40)} = 2.9^{[q]}$, $P < 0.05$; density index, n = 53, $P \geq 0.05$; d) Adults of *M. vitrata* per flower, n = 66, $P \geq 0.05$; density index, n = 53, $P \geq 0.05$.

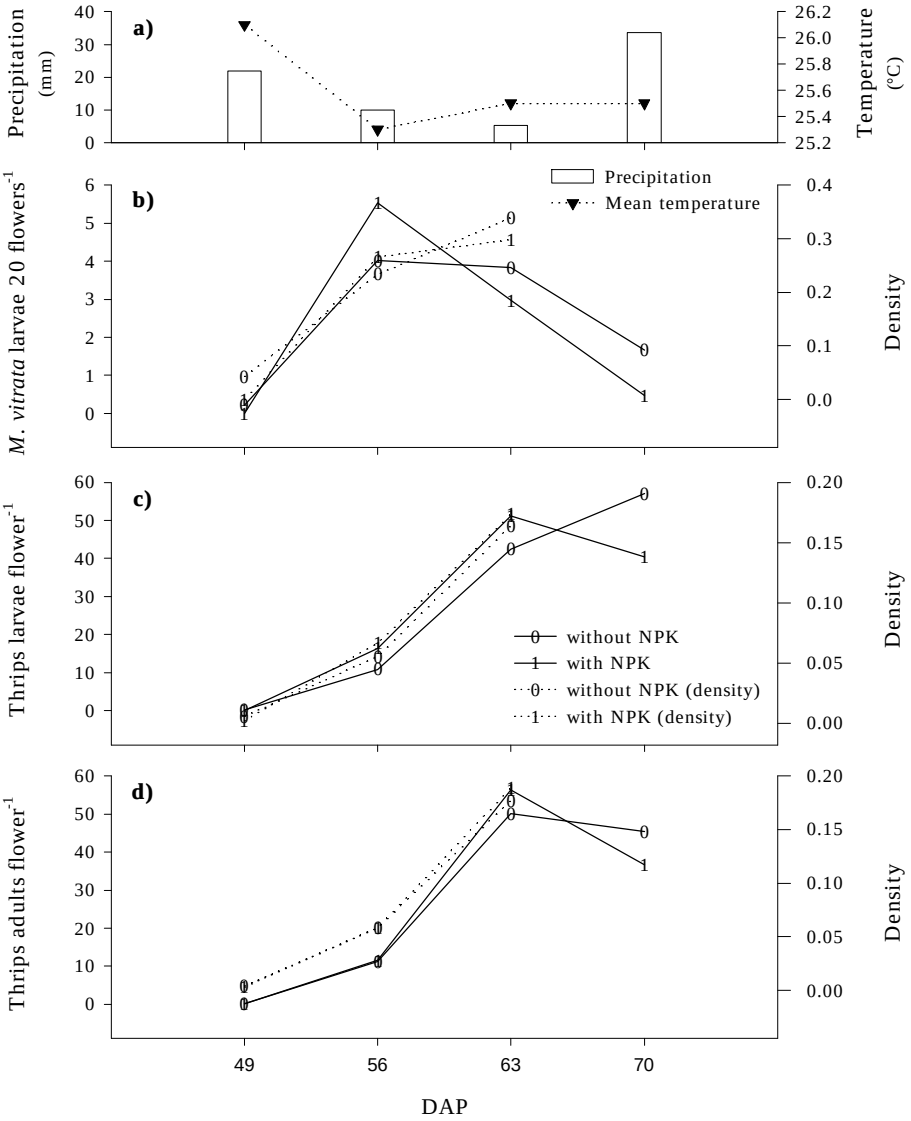


Fig. 3.2. Tokpa/Ayou, season II/95, sampling interval DAP 42-77: a) Precipitation (ð) (sum of preceding week in mm) and mean temperature (···) (weekly mean of preceding week in °C); b)-d) Population dynamics as abundance (⁻) and density index (···) (number of insects per flower, actual counts on phenology) (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Larvae of *M. vitrata* per 20 flowers, n = 72, $P \geq 0.05$, density index, NPK*mulch interaction main effect, n = 52, $F_{(2,32)} = 3.7$, $P < 0.05$; c) Larvae of *M. sjostedti* per flower, n = 108, $P \geq 0.05$; density index, n = 68, $P \geq 0.05$; d) Adults of *M. vitrata* per flower, n = 108, $P \geq 0.05$; density index, NPK main effect, n = 67, $F_{(1,41)} = 5.5$, $P < 0.05$.

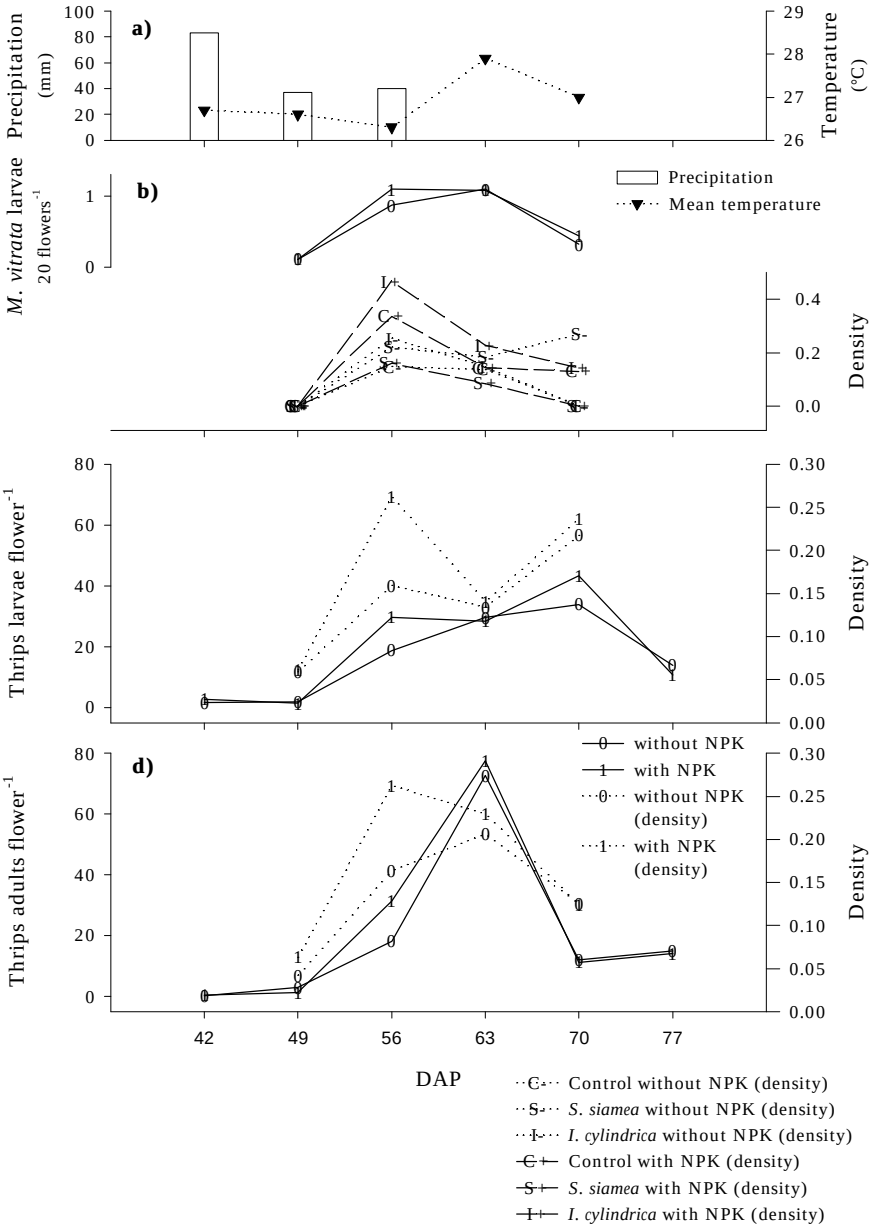


Fig. 3.3. Tokpa/Ayou, season I/96, sampling interval DAP 42-77: a) Precipitation (ð) (sum of preceding week in mm) and mean temperature (¨) (weekly mean of preceding week in °C); b)-d) Population dynamics as abundance (⁻) and density index (¨) (number of insects per flower, actual counts on phenology) (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Larvae of *M. vitrata* per 20 flowers, n = 89, $P \geq 0.05$; density index density, n = 53, $P \geq 0.05$; c) Larvae of *M. sjostedti* per flower, n = 72, $P \geq 0.05$; density index, n = 66, $P \geq 0.05$; d) Adults of *M. vitrata* per flower, trend on NPK, n = 107, $F_{(1,69)} = 7.0$, $P = 0.01$; density index, n = 66, $P \geq 0.05$.

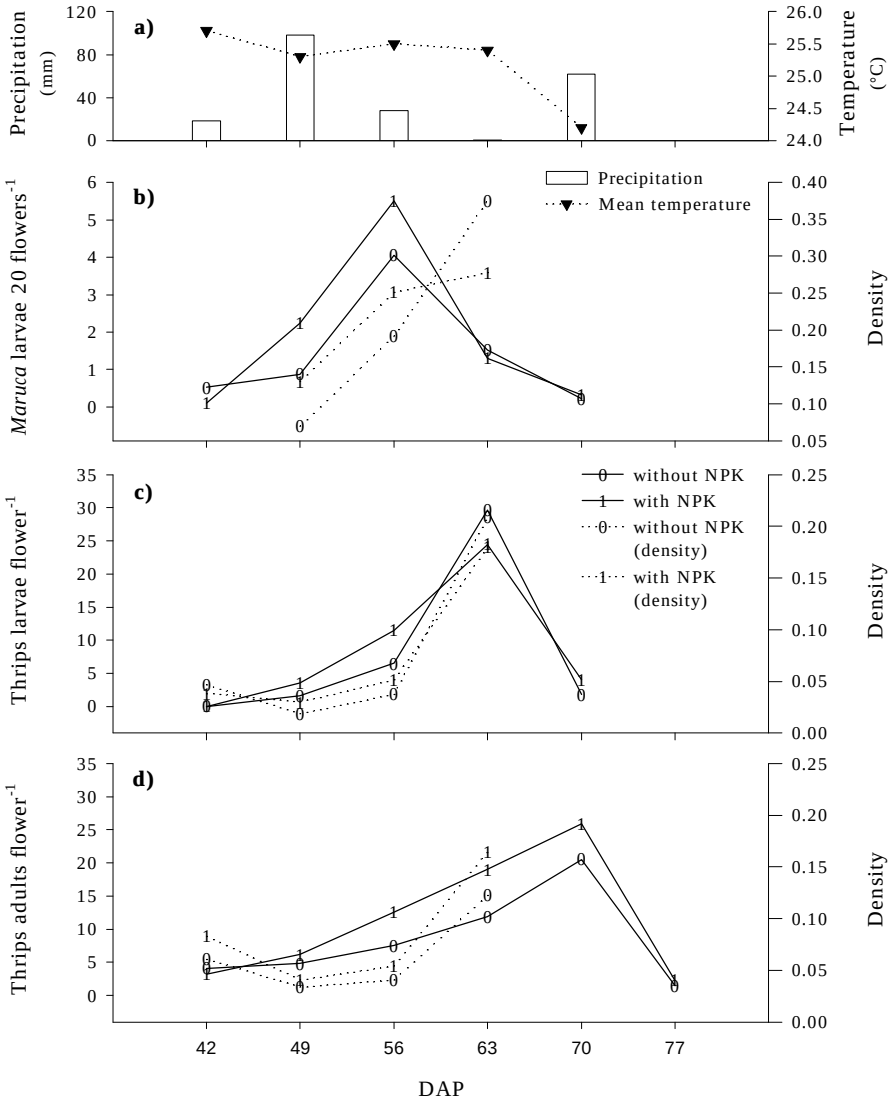


Fig. 3.4. Tokpa/Ayou, season II/96, sampling interval DAP 49-84: a) Precipitation (ð) (sum of preceding week in mm) and mean temperature (¨) (weekly mean of preceding week in °C); b)-d) Population dynamics as abundance (⁻) and density index (¨) (number of insects per flower, actual counts on phenology) (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Larvae of *M. vitrata* per 20 flowers, n = 54, $P \geq 0.05$; density index, n = 54, $P \geq 0.05$; c) Larvae of *M. sjostedti* per flower, n = 90, $P \geq 0.05$; density index, n = 68, $P \geq 0.05$; d) Adults of *M. vitrata* per flower, trend on NPK, n = 108, $F_{(5,70)} = 3.3^{[1]}$, $P < 0.05$; density index, n = 68, $P \geq 0.05$.

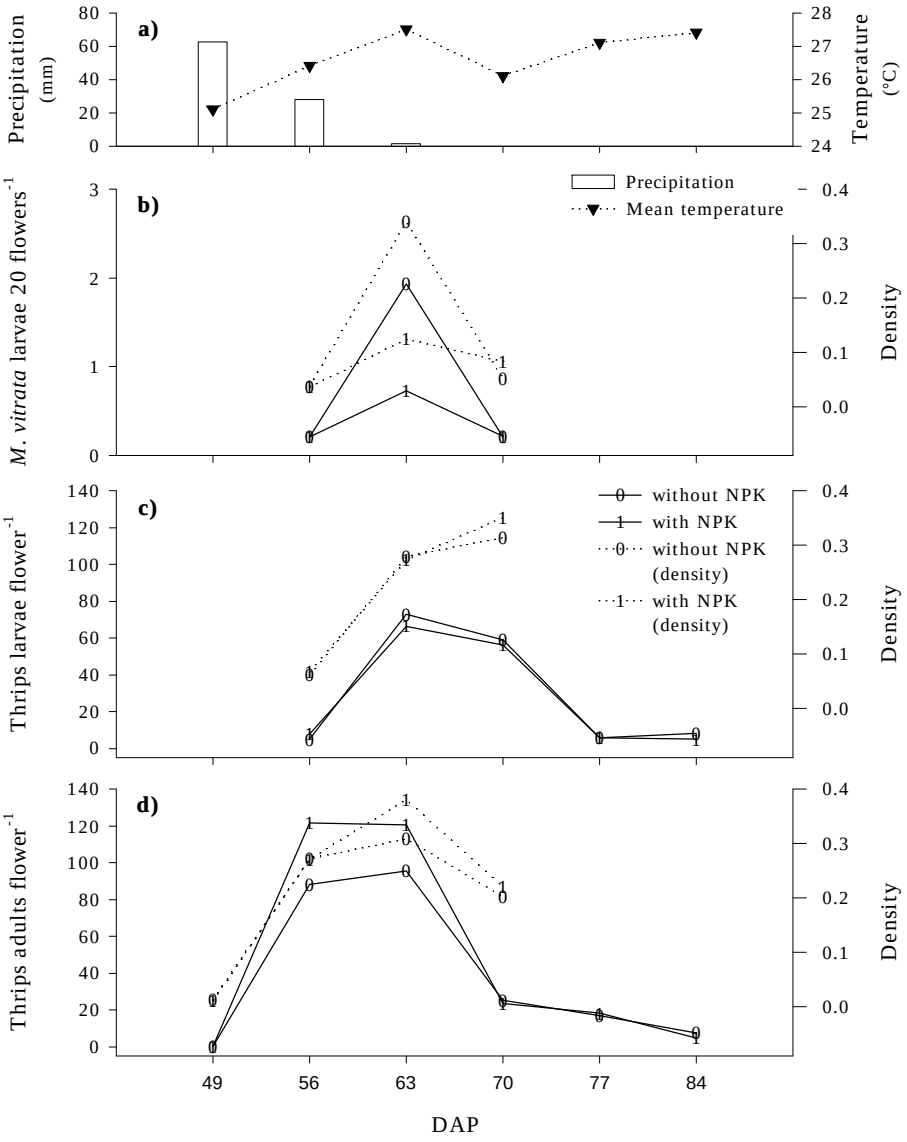


Fig. 3.5. Tokpa/Ayou, season I/97, sampling interval DAP 35-91: a) Precipitation (ð) (sum of preceding week in mm) and mean temperature (¨) (weekly mean of preceding week in °C); b)-d) Population dynamics as abundance (⁻) and density index (¨) (number of insects per flower, actual counts on phenology) (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Larvae of *M. vitrata* per 20 flowers, n = 72, $P \geq 0.05$; density index, mulch main effect, n = 72, $F_{(2,46)} = 3.6$, $P < 0.05$; c) Larvae of *M. sjostedti* per flower, n = 126, $P \geq 0.05$; density index: trend on NPK*mulch interaction, n = 88, $F_{(8,56)} = 2.2$, $P < 0.05$; d) Adults of *M. vitrata* per flower, NPK main effect, n = 162, $F_{(1,106)} = 4.1$, $P < 0.05$; density index, n = 88, $P \geq 0.05$.

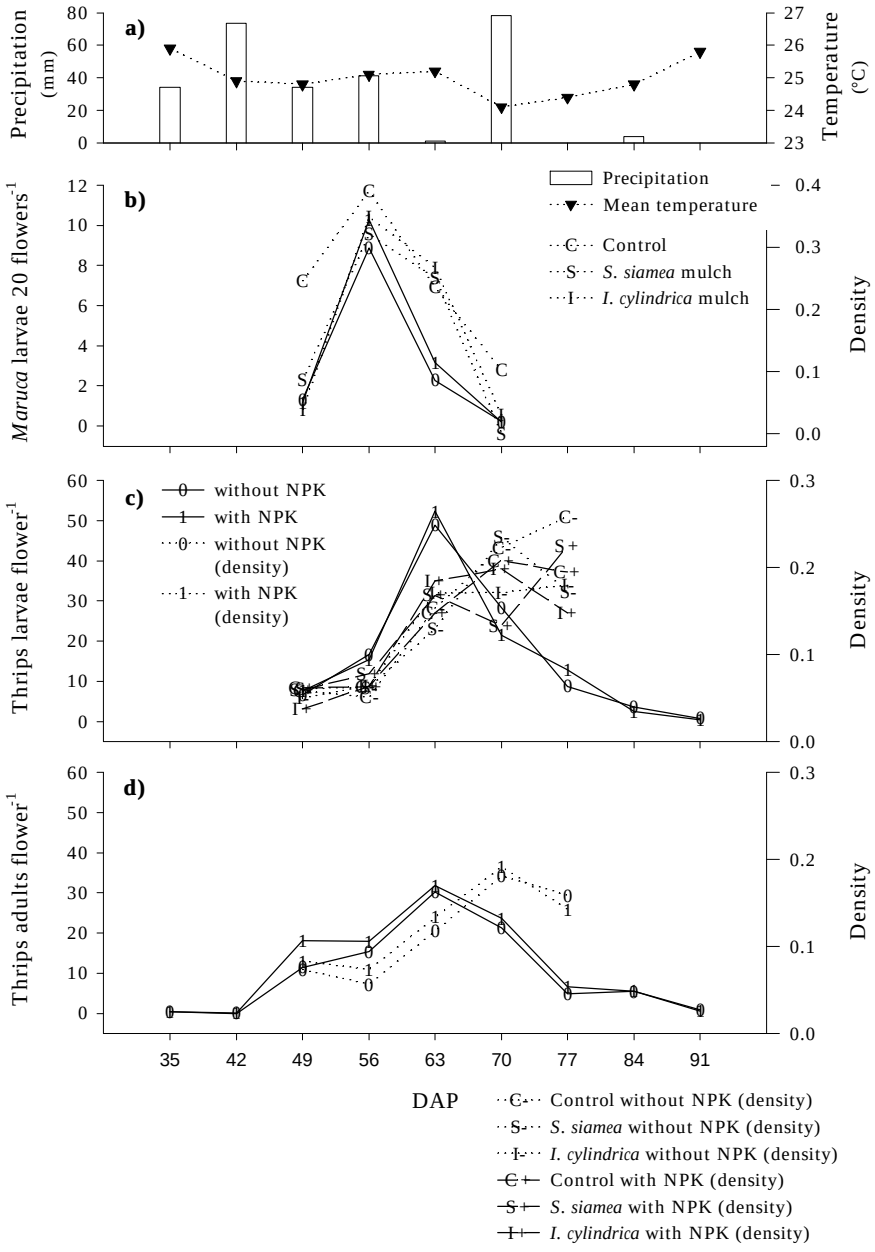


Fig. 3.6. Lema, season I/95, sampling interval DAP 42-63: a) Precipitation (ð) (sum of preceding week in mm) and mean temperature (¨) (weekly mean of preceding week in °C); b)-d) Population dynamics as abundance (¯) and density index (¨) (number of insects per flower, actual counts on phenology) (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Larvae of *M. vitrata* per 20 flowers, n = 72, $P \geq 0.05$; density index, n = 72, $P \geq 0.05$; c) Larvae of *M. sjostedti* per flower, n = 64, $P \geq 0.05$; density index, n = 64, $P \geq 0.05$; d) Adults of *M. sjostedti* per flower, n = 78, $P \geq 0.05$; density index, n = 64, $P \geq 0.05$.

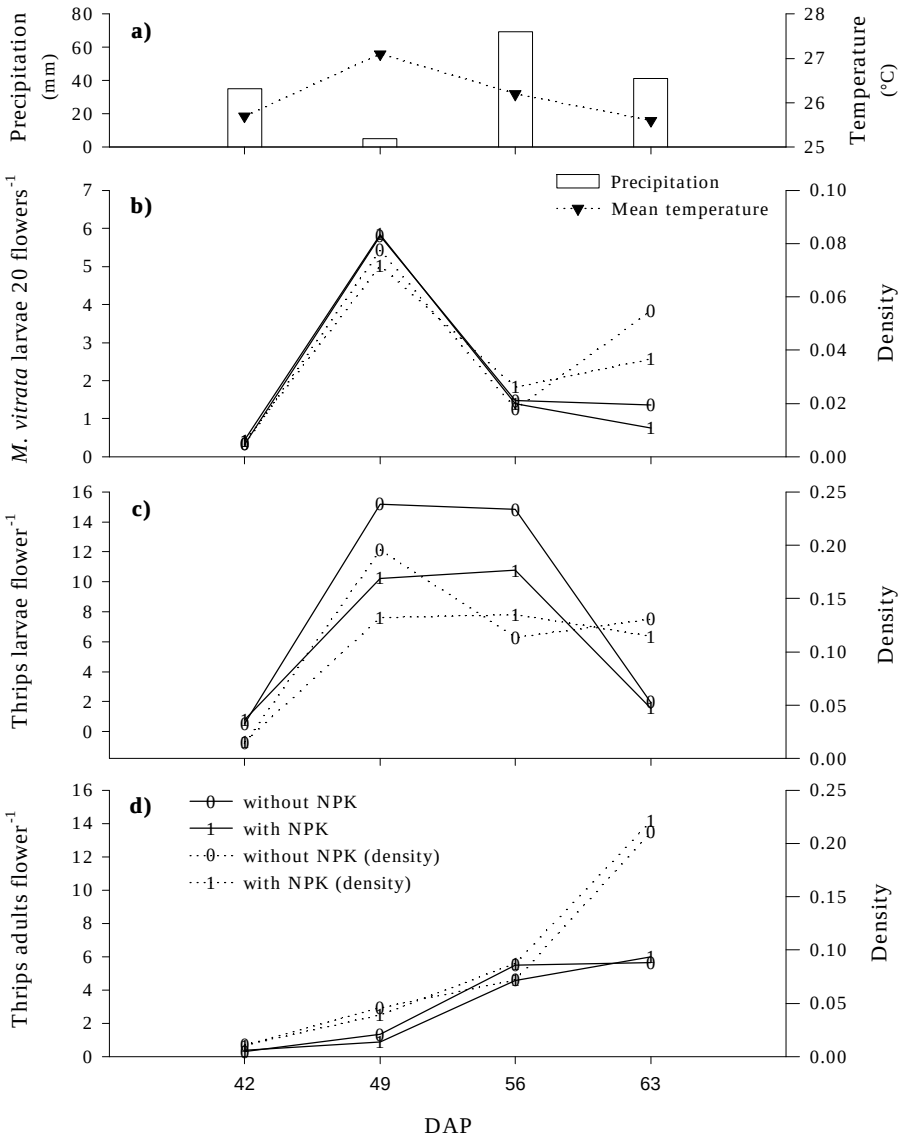


Fig. 3.7. Lema, season II/95, sampling interval DAP 42-70: a) Precipitation (ð) (sum of preceding week in mm) and mean temperature (¨) (weekly mean of preceding week in °C); b)-d) Population dynamics as abundance (⁻) and density index (¨) (number of insects per flower, actual counts on phenology) (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Larvae of *M. vitrata* per 20 flowers, n = 72, $P \geq 0.05$; density index, NPK main effect, n = 59, $F_{(1,33)} = 4.4$, $P < 0.05$; c) Larvae of *M. sjostedti* per flower, n = 64, $P \geq 0.05$; density index, n = 42, $P \geq 0.05$; d) Adults of *M. sjostedti* per flower, n = 64, $P \geq 0.05$; density index, n = 42, $P \geq 0.05$.

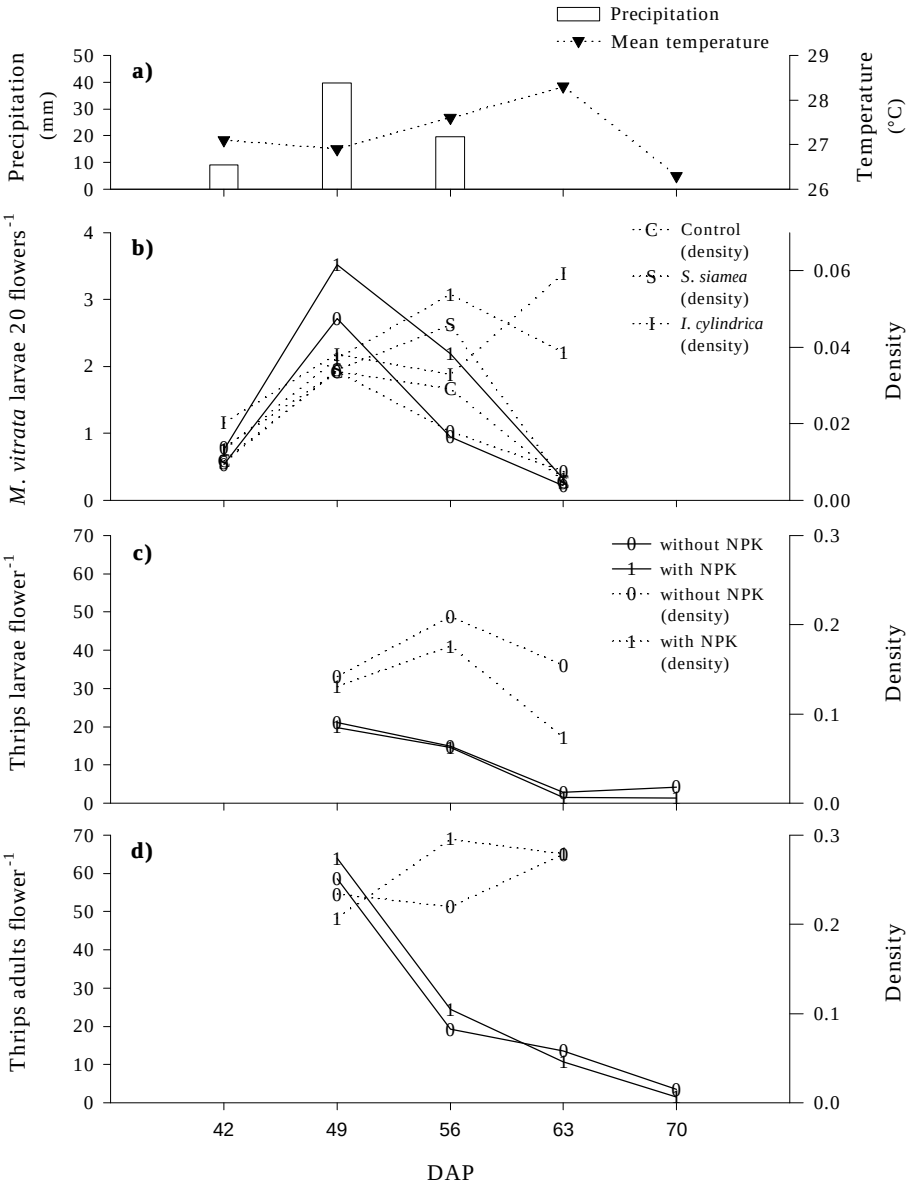


Fig. 3.8. Lema, season I/96, sampling interval DAP 35-77: a) Precipitation (ð) (sum of preceding week in mm) and mean temperature (¨) (weekly mean of preceding week in °C); b)-d) Population dynamics as abundance (⁻) and density index (¨) (number of insects per flower, actual counts on phenology) (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Larvae of *M. vitrata* per 20 flowers, NPK main effect, n = 90, $F_{(1,58)} = 22.8$, $P << 0.01$; density index, NPK main effect, n = 85, $F_{(1,53)} = 4.4$, $P < 0.05$; c) Larvae of *M. sjostedti* per flower, trend on NPK, n = 126, $F_{(6,82)} = 2.6^{[l]}$, $P < 0.05$; density index, trend on NPK, n = 42, $F_{(4,53)} = 6.0^{[l]}$, $P < 0.01$; d) Adults of *M. sjostedti* per flower, NPK main effect, n = 126, $F_{(1,82)} = 7.5$, $P < 0.01$; density index, n = 85, $P \geq 0.05$.

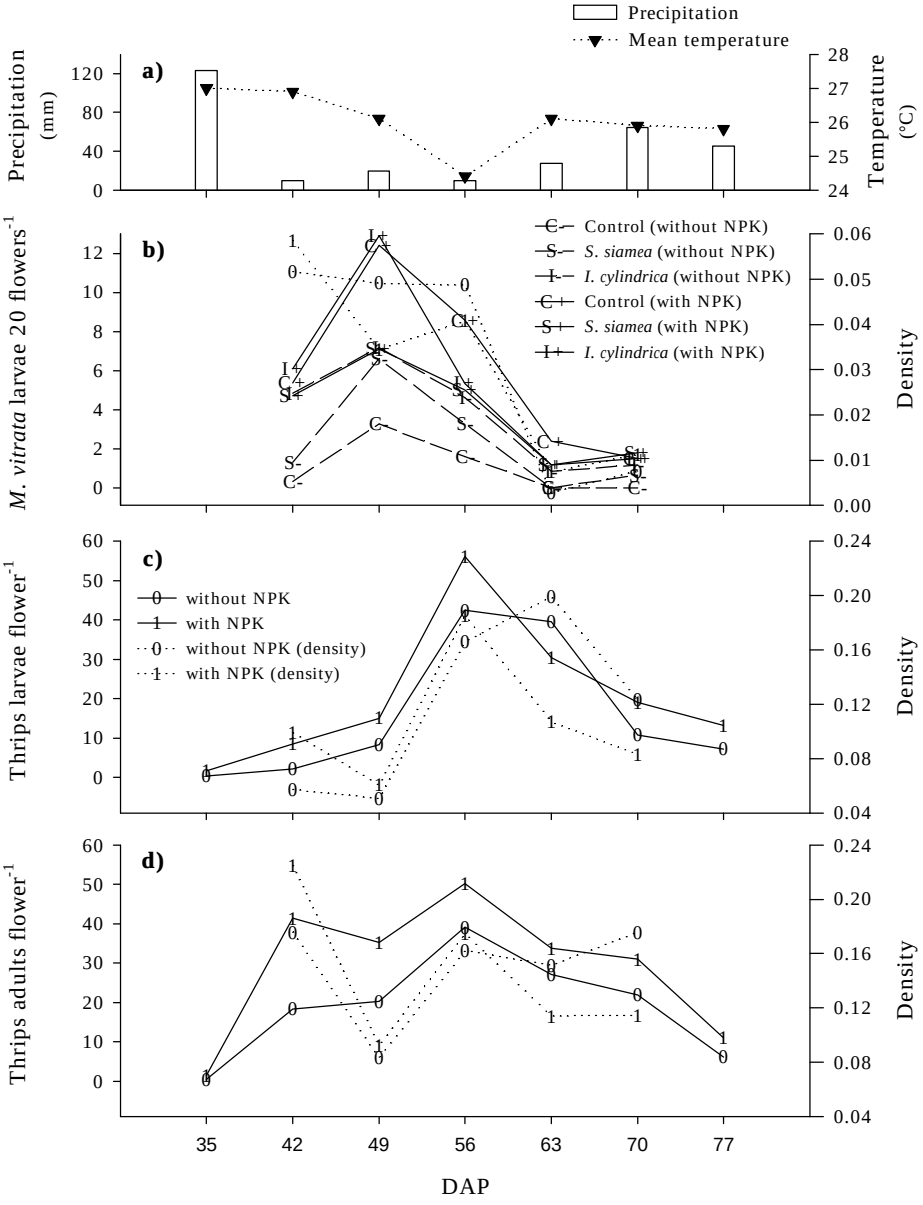


Fig. 3.9. Lema, season II/96, sampling interval DAP 35-77: a) Precipitation (ð) (sum of preceding week in mm) and mean temperature (···) (weekly mean of preceding week in °C); b)-d) Population dynamics as abundance (–) and density index (···) (number of insects per flower, actual counts on phenology) (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Larvae of *M. vitrata* per 20 flowers, NPK main effect, n = 54, $F_{(1,34)} = 5.6$, $P < 0.05$; density index, trend on mulch, n = 46, $F_{(4,26)} = 5.2^{[l]}$, $P < 0.01$; c) Larvae of *M. sjostedti* per flower, trend on NPK, n = 124, $F_{(6,80)} = 5.8^{[l]}$, $P << 0.01$; density index, trend on NPK, n = 48, $F_{(2,28)} = 3.6^{[l]}$, $P < 0.05$; d) Adults of *M. sjostedti* per flower, trend on NPK, n = 124, $F_{(6,80)} = 4.3^{[l]}$, $P < 0.01$; density index, NPK main effect, n = 48, $F_{(1,28)} = 6.8^{[l]}$, $P < 0.05$.

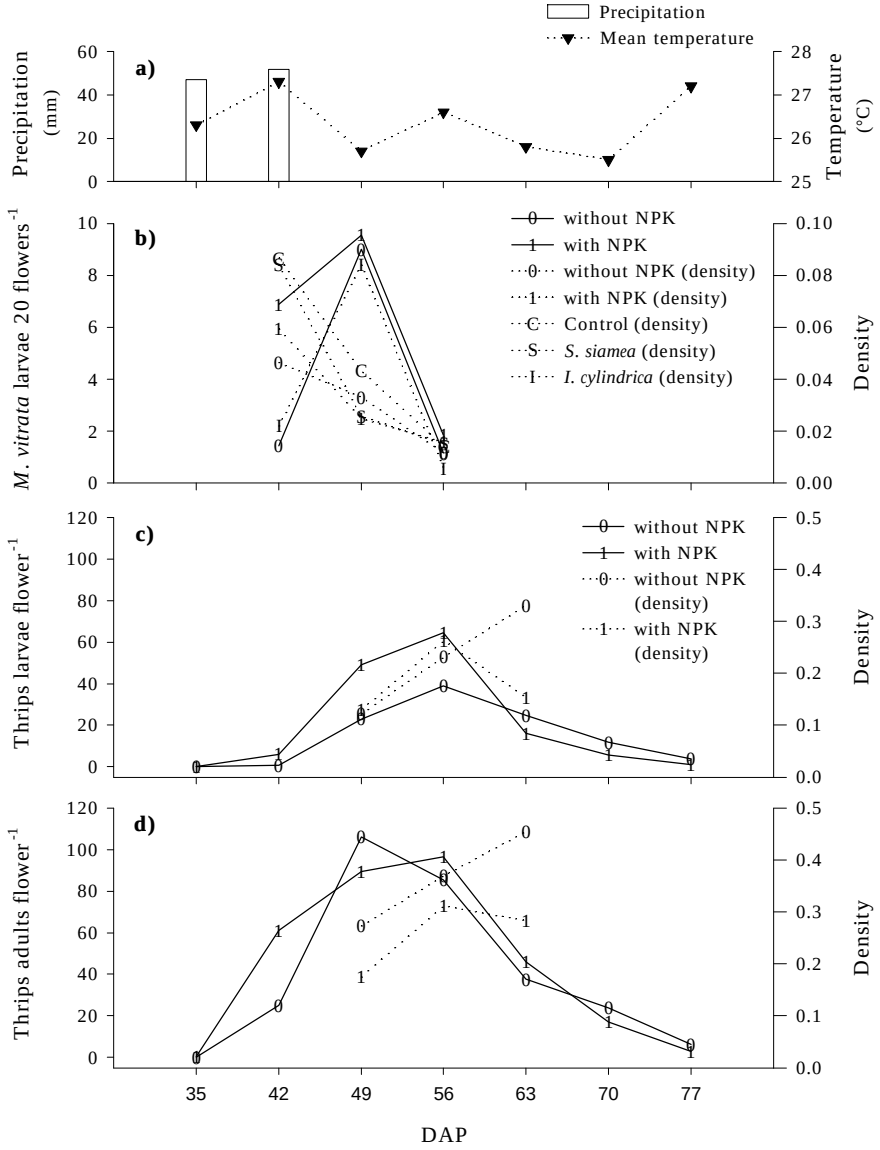


Fig. 3.10. Lema, season I/97, sampling interval DAP 35-91: a) Precipitation (ð) (sum of preceding week in mm) and mean temperature (···) (weekly mean of preceding week in °C); b)-d) Population dynamics as abundance (⁻) and density index (···) (number of insects per flower, actual counts on phenology) (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Larvae of *M. vitrata* per 20 flowers, n = 106, $P \geq 0.05$; density index, trend on NPK*mulch, n = 66, $F_{(6,40)} = 2.4^{[q]}$, $P < 0.05$; c) Larvae of *M. sjostedti* per flower, trend on NPK, n = 160, $F_{(8,104)} = 2.5^{[l]}$, $P < 0.05$, trend on mulch, n = 160, $F_{(16,104)} = 2.9^{[q]}$, $P < 0.01$; density index, NPK*mulch interaction, n = 83, $F_{(2,51)} = 4.9$, $P < 0.05$; d) Adults of *M. sjostedti* per flower, trend on NPK*mulch, n = 160, $F_{(16,104)} = 1.9$, $P < 0.05$; density index, NPK*mulch interaction, n = 83, $F_{(2,51)} = 3.3$, $P < 0.05$.

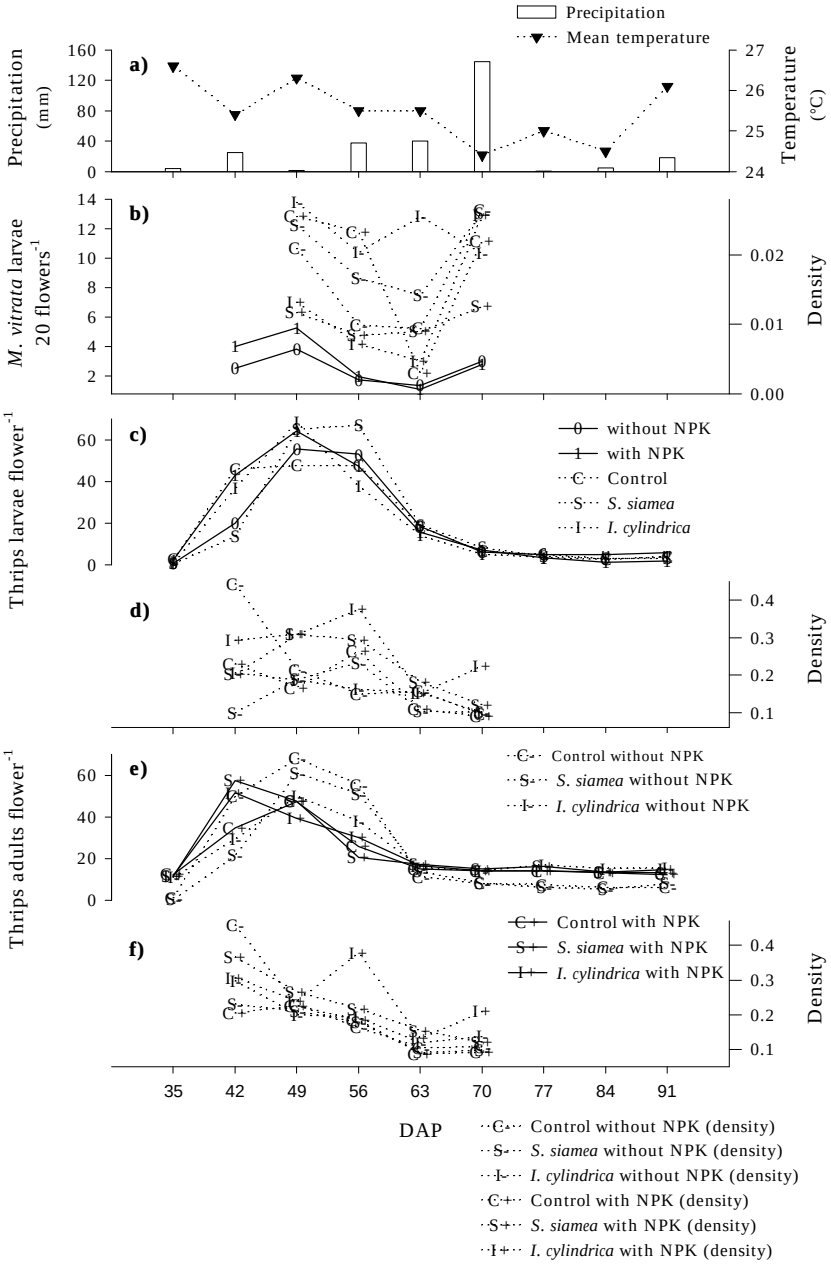


Fig. 3.11. IITA, season I/95, sampling interval DAP 42-70: a) Precipitation (ð) (sum of preceding week in mm) and mean temperature (¨) (weekly mean of preceding week in °C); b)-d) Population dynamics as abundance (–) and density index (¨) (number of insects per flower, actual counts on phenology) (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Larvae of *M. vitrata* per 20 flowers, n = 36, $P \geq 0.05$; density index, n = 35, $P \geq 0.05$; c) Larvae of *M. sjostedti* per flower, n = 55, $P \geq 0.05$; density index, n = 47, $P \geq 0.05$; d) Adults of *M. sjostedti* per flower, n = 43, $P \geq 0.05$; density index, trend on mulch, n = 47, $F_{(6,40)} = 2.4^{[q]}$, $P < 0.05$.

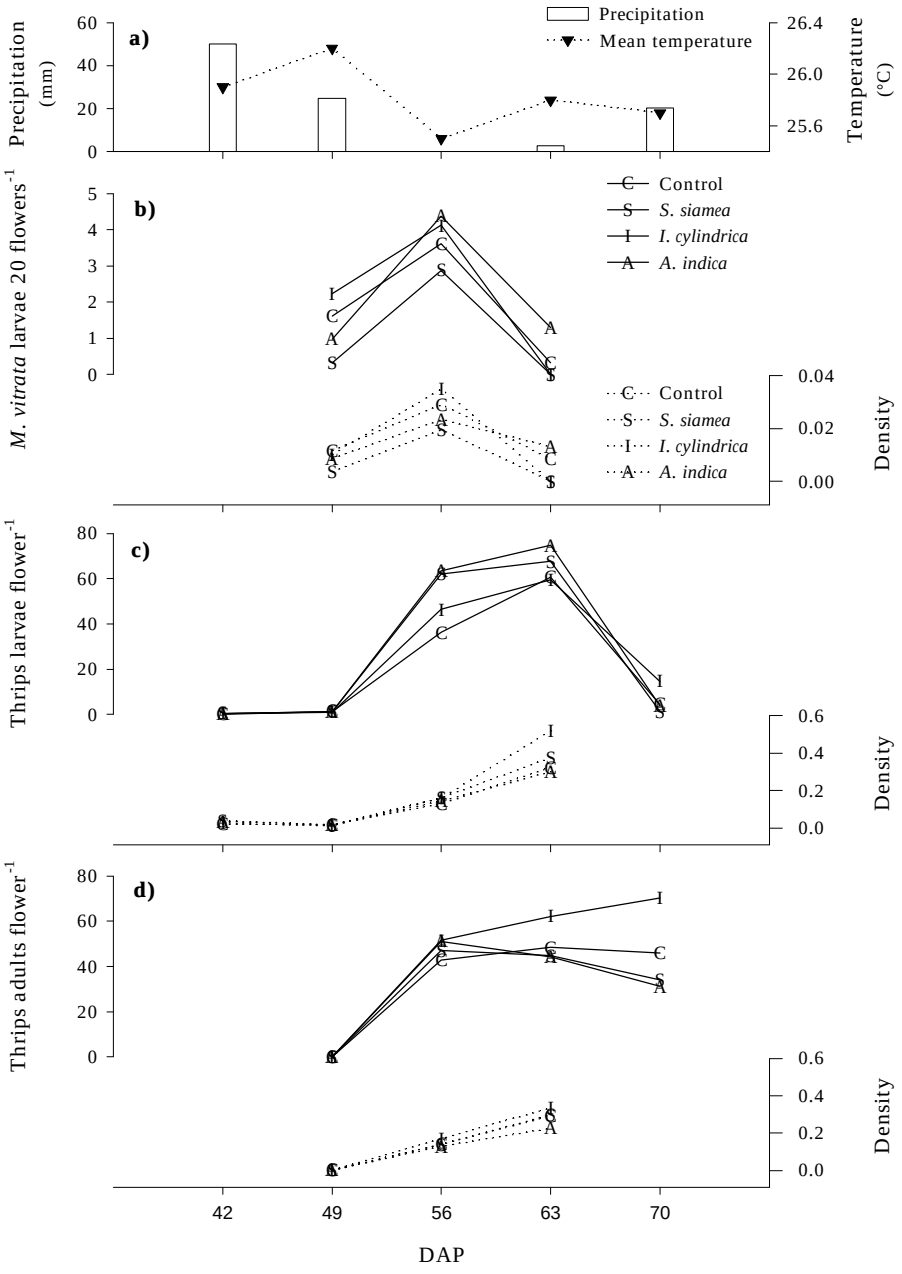


Fig. 3.12. IITA, season II/95, sampling interval DAP 42-77: a) Precipitation (ð) (sum of preceding week in mm) and mean temperature (···) (weekly mean of preceding week in °C); b)-d) Population dynamics as abundance (⁻) and density index (···) (number of insects per flower, actual counts on phenology) (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Larvae of *M. vitrata* per 20 flowers, n = 36, $P \geq 0.05$; density index, n = 36, $P \geq 0.05$; c) Larvae of *M. sjostedti* per flower, trend on mulch, n = 72, $F_{(15,46)} = 2.0^{[q]}$, $P < 0.05$; density index, trend on mulch, n = 57, $F_{(12,35)} = 3.6^{[q]}$, $P < 0.01$; d) Adults of *M. sjostedti* per flower, mulch main effect, n = 72, $F_{(3,46)} = 7.7$, $P < 0.01$, density index, mulch main effect, n = 57, $P \geq 0.05$.

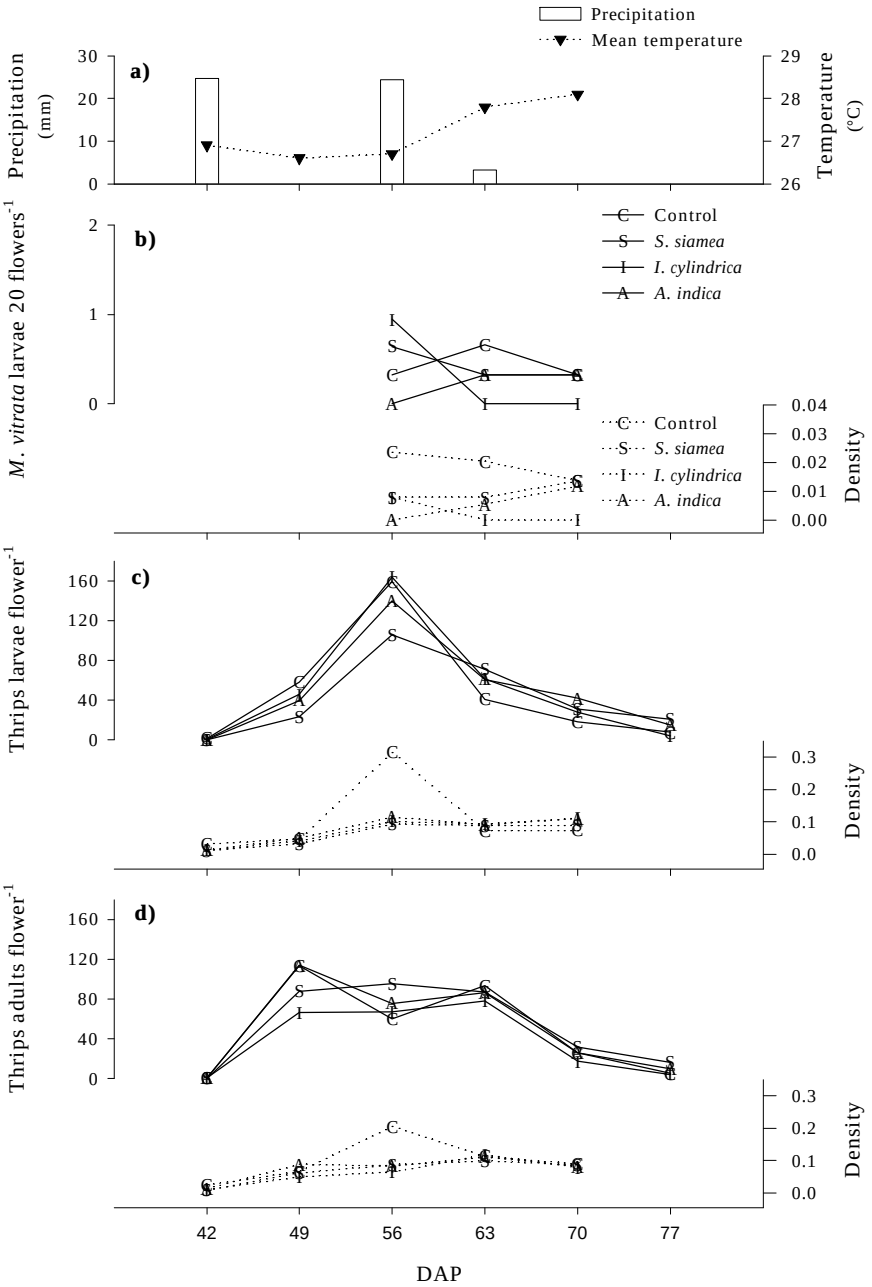


Fig. 3.13. IITA, season I/96, sampling interval DAP 35-77: a) Precipitation (ð) (sum of preceding week in mm) and mean temperature (¨) (weekly mean of preceding week in °C); b)-d) Population dynamics as abundance (–) and density index (¨) (number of insects per flower, actual counts on phenology) (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Larvae of *M. vitrata* per 20 flowers, mulch main effect, n = 59, $F_{(3,37)} = 4.1$, $P < 0.05$; density index, mulch main effect, n = 55, $F_{(3,33)} = 2.9$, $P < 0.05$; c) Larvae of *M. sjostedti* per flower, n = 83, $P \geq 0.05$; density index, n = 48, $P \geq 0.05$; d) Adults of *M. sjostedti* per flower, n = 83, $P \geq 0.05$; density index, n = 48, $P \geq 0.05$.

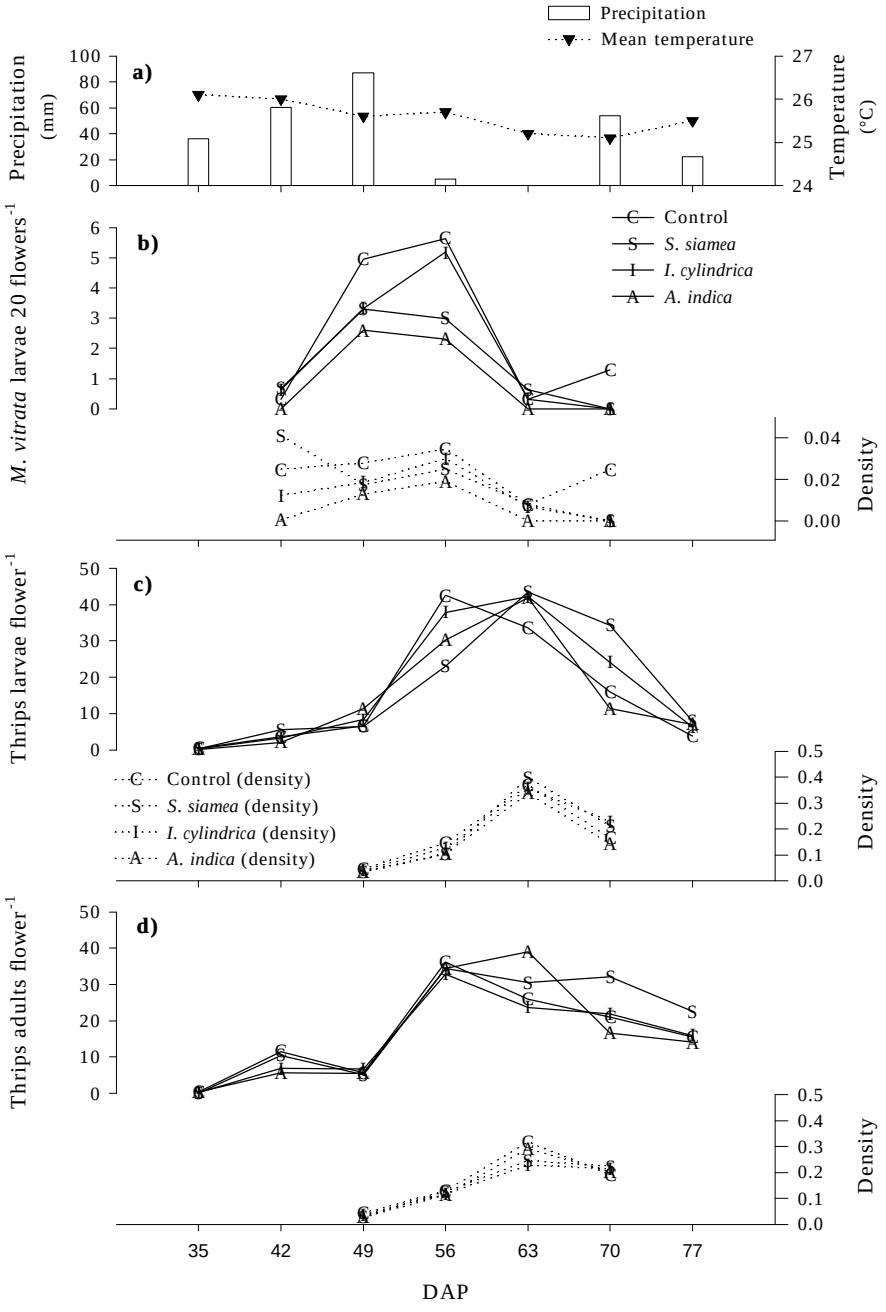


Fig. 3.14. IITA, season II/96, sampling interval DAP 42-77: a) Precipitation (ð) (sum of preceding week in mm) and mean temperature (···) (weekly mean of preceding week in °C); b)-d) Population dynamics as abundance (⁻) and density index (···) (number of insects per flower, actual counts on phenology) (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Larvae of *M. vitrata* per 20 flowers, n = 24, $P \geq 0.05$; density index, n = 18, $P \geq 0.05$; c) Larvae of *M. sjostedti* per flower, trend on mulch, n = 70, $F_{(15,44)} = 2.8$, $P < 0.01$; density index, trend on mulch, n = 22, $F_{(3,12)} = 6.1$, $P < 0.01$; d) Adults of *M. sjostedti* per flower, n = 70, $P \geq 0.05$; density index, trend on mulch, n = 22, $F_{(3,12)} = 4.6$, $P < 0.05$.

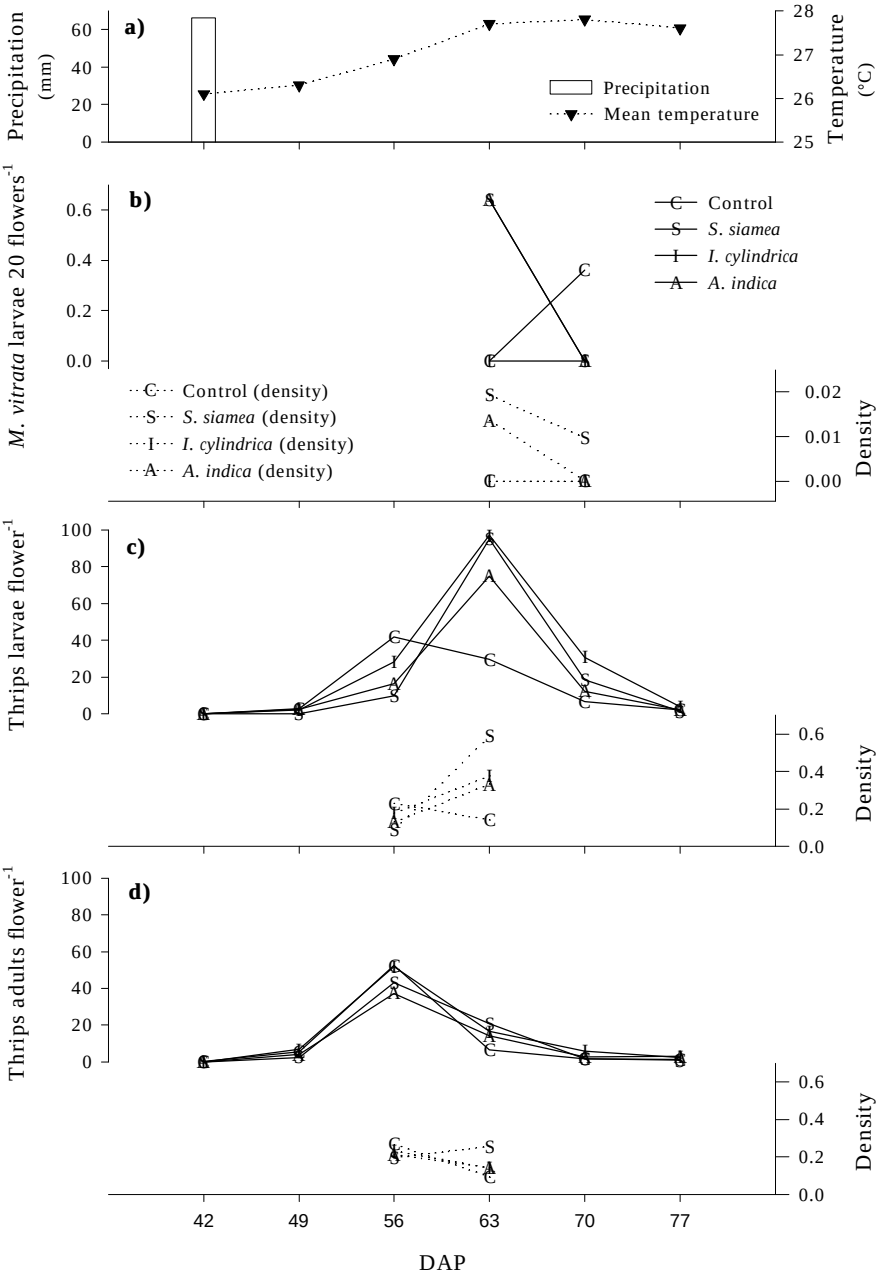


Fig. 3.15. IITA, season I/97, sampling interval DAP 35-91: a) Precipitation (ð) (sum of preceding week in mm) and mean temperature (¨) (weekly mean of preceding week in °C); b)-d) Population dynamics as abundance (–) and density index (¨) (number of insects per flower, actual counts on phenology) (detransformed data): effects of NPK, with (1)/ without (0) NPK, and mulch, *S. siamea* (S) and *I. cylindrica* (I), against the control (C): b) Larvae of *M. vitrata* per 20 flowers, n = 48, $P \geq 0.05$; density index, n = 34, $P \geq 0.05$; c) Larvae of *M. sjostedti* per flower, n = 80, $P \geq 0.05$; density index, n = 34, $P \geq 0.05$; d) Adults of *M. sjostedti* per flower, trend on mulch profiles, n = 104, $F_{(24,66)} = 2.3$, $P < 0.01$; density index, n = 34, $P \geq 0.05$.

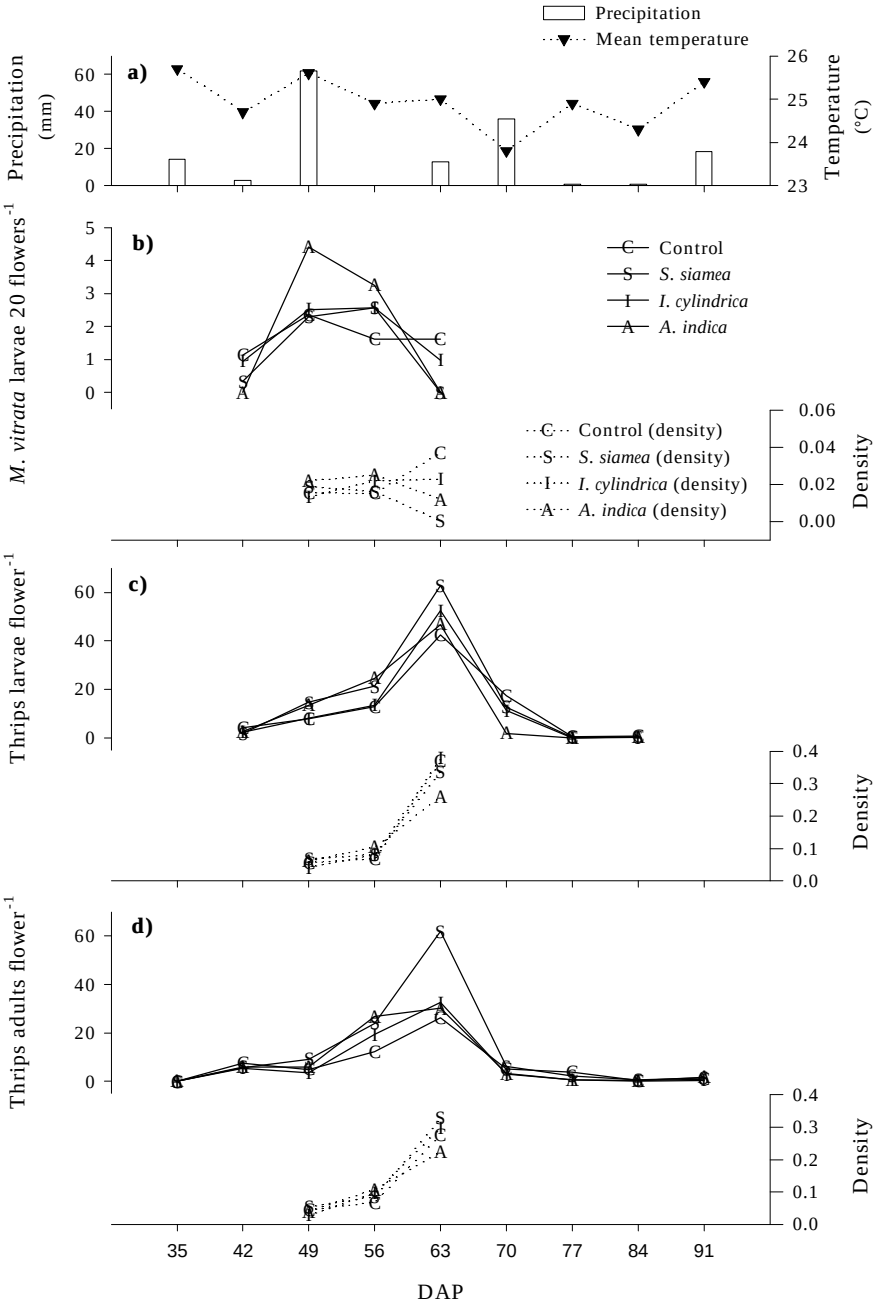


Fig. 4.1. Parasitization rate of larvae of *M. vitrata* (a) and *M. sjostedti* (b) in flowers of cowpea: relation between larval density per plot (treatment) and parasitism rate in percent. Data are pooled across three regions and five seasons under the assumption that the underlying density-dependence does not generally change among regions and seasons. Densities per plot (number of larvae per plot) are calculated using larval numbers per flower (mean scores), flowers per plant (mean scores), plants per plot (mean scores) and relative mortalities of larvae obtained from a fixed volume of flowers per plot. All measures used together are obtained from the same plot at the same sampling day. Cases of parasitism where no larvae were found in flowers (subsamples of 20 flowers per plot) or where no flowers were counted (subsamples of 10 plants per plot) were discarded. a) Larvae of *M. vitrata*, n (cases) = 520, total number of larvae estimated on the basis of subsamples = 273,548; b) Larvae of *M. sjostedti*, n = 860, total number of larvae estimated on the basis of subsamples = 43,414,478.

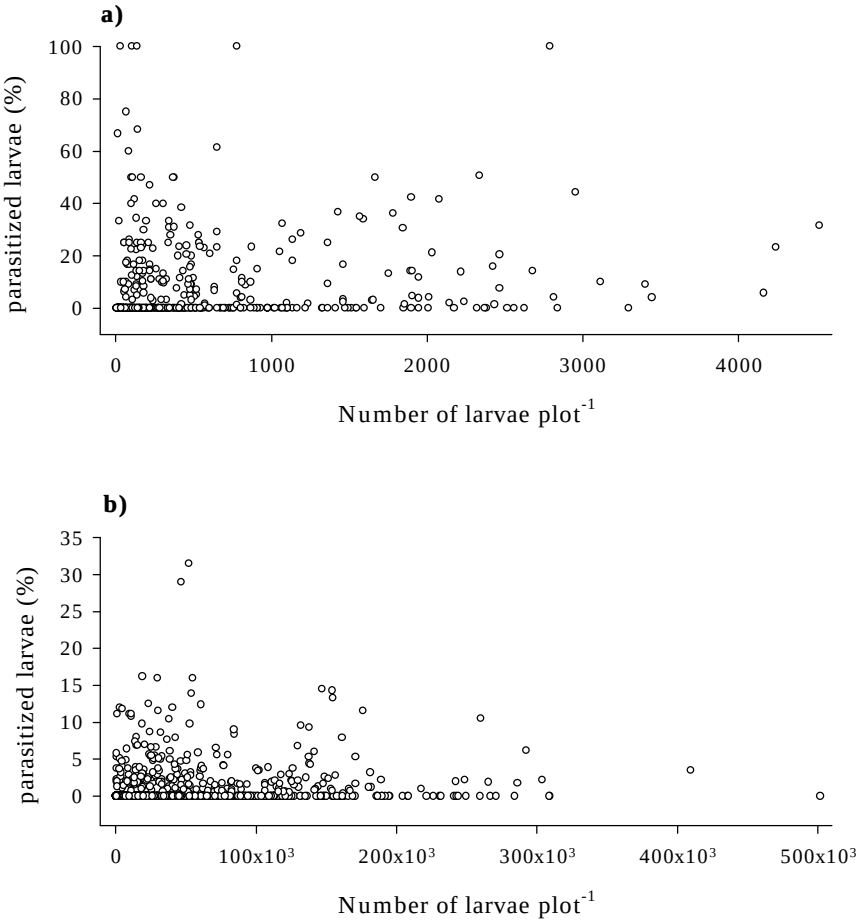


Fig. 7.1. Lema, season II/96, population dynamics in alternative host plants, larvae of *M. vitrata* in cowpea compared with 3 species of alternative hosts. Values are means per 50 flowers of the respective plant species, values for cowpea are extrapolated to the same sample size.

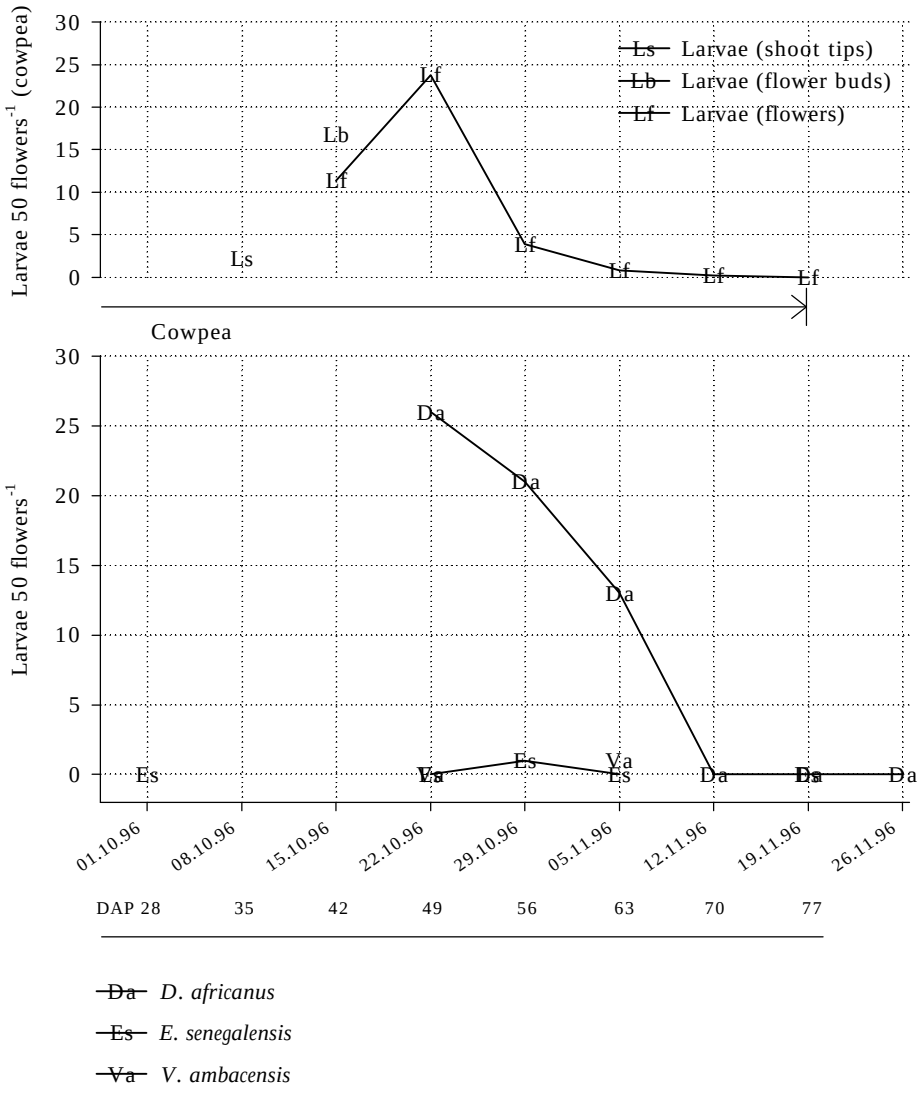


Fig. 7.2. Tokpa/Ayou, season I/95, population dynamics in alternative host plants, larvae and adults of *M. sjostedti* in 6 species of alternative hosts. Values are means per flower. The onset of cowpea cultivation is indicated by the respective DAP.

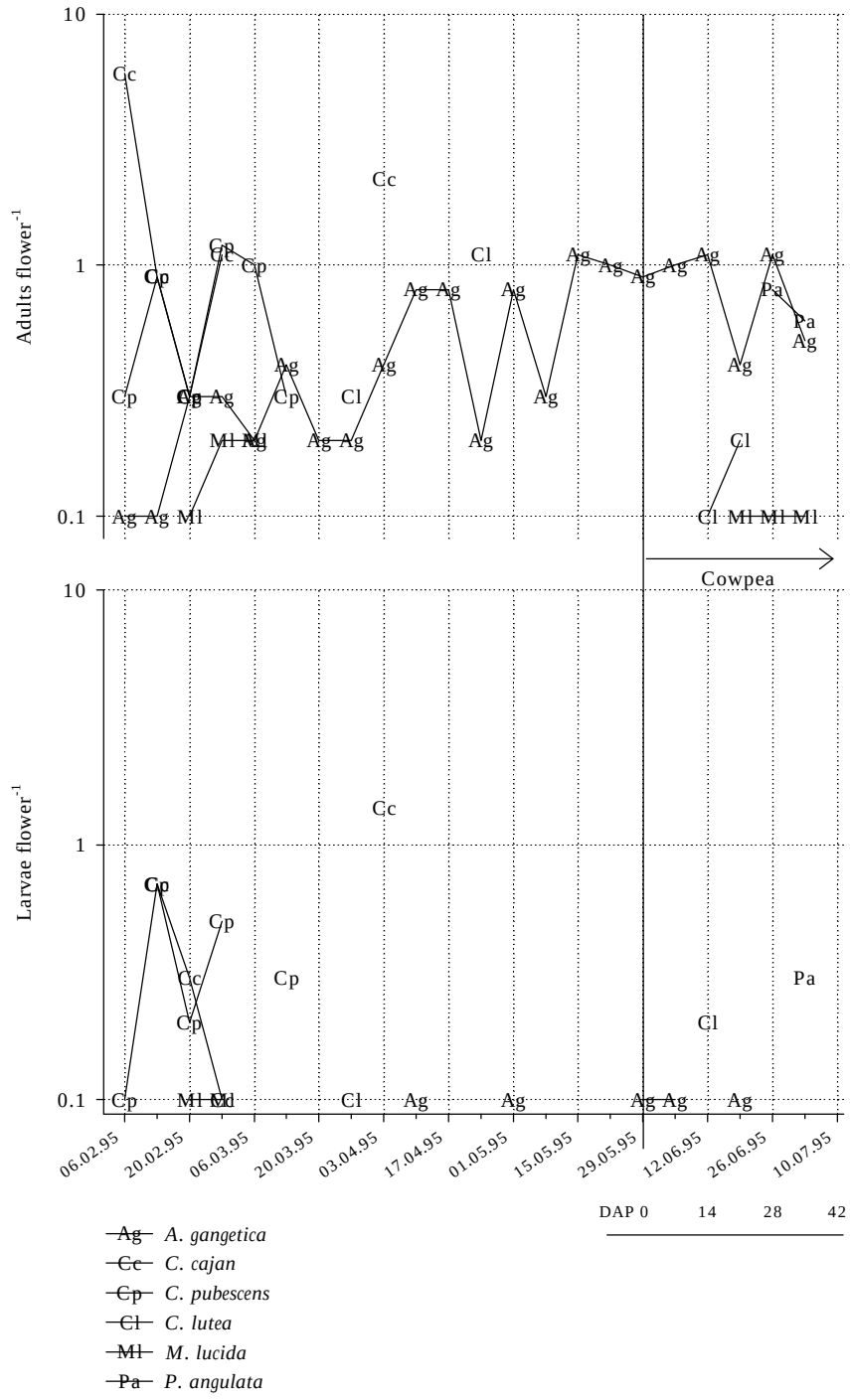


Fig. 7.3. Tokpa/Ayou, season II/95, population dynamics in alternative host plants, larvae and adults of *M. sjostedti* in cowpea compared with 5 species of alternative hosts. Values are means per flower, they were pooled across treatments for cowpea (larvae, adults), St = shoot tips, Fb = flower buds. The onset of cowpea cultivation is indicated by the respective DAP.

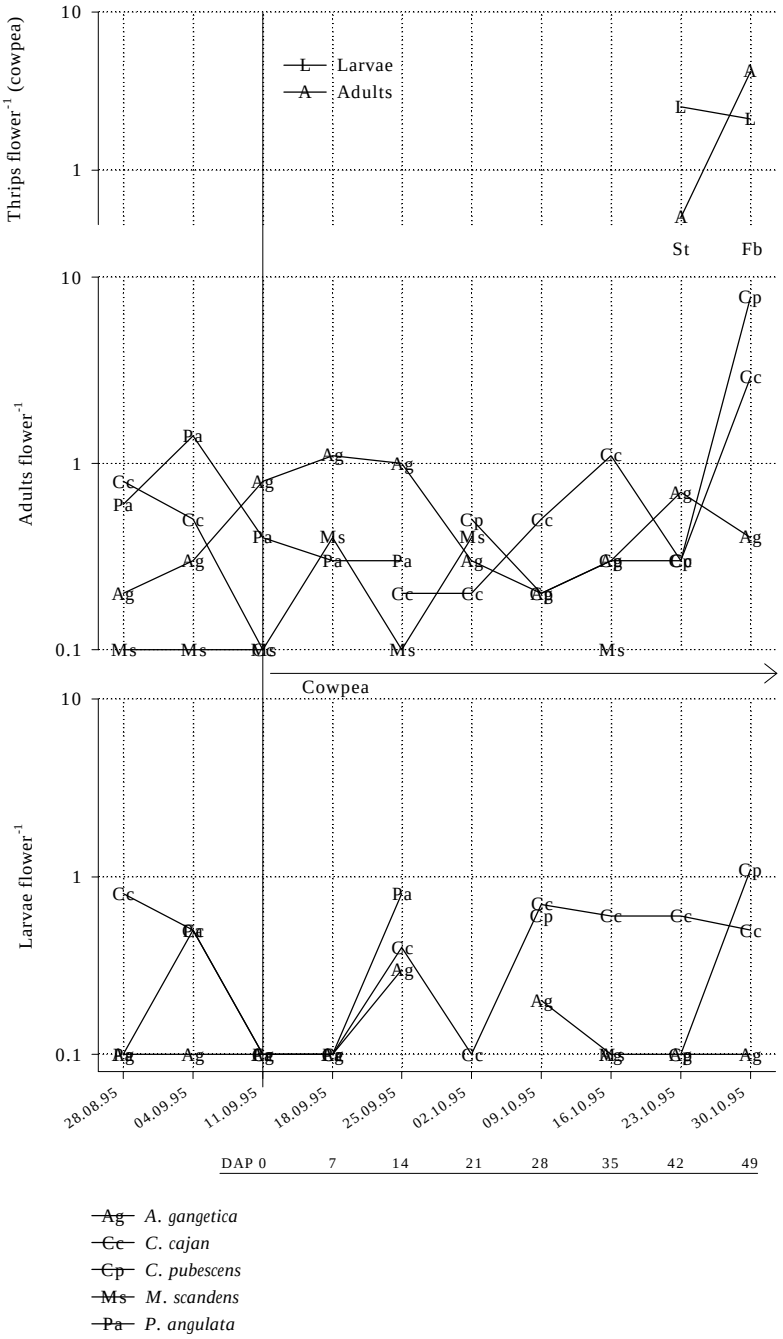


Fig. 7.4. Tokpa/Ayou, season I/96, population dynamics in alternative host plants, larvae and adults of *M. sjostedti* in cowpea compared with 5 species of alternative hosts. Values are means per flower, they were pooled across treatments for cowpea (larvae, adults), St = shoot tips, Fb = flower buds, F = flowers. The onset of cowpea cultivation is indicated by the respective DAP.

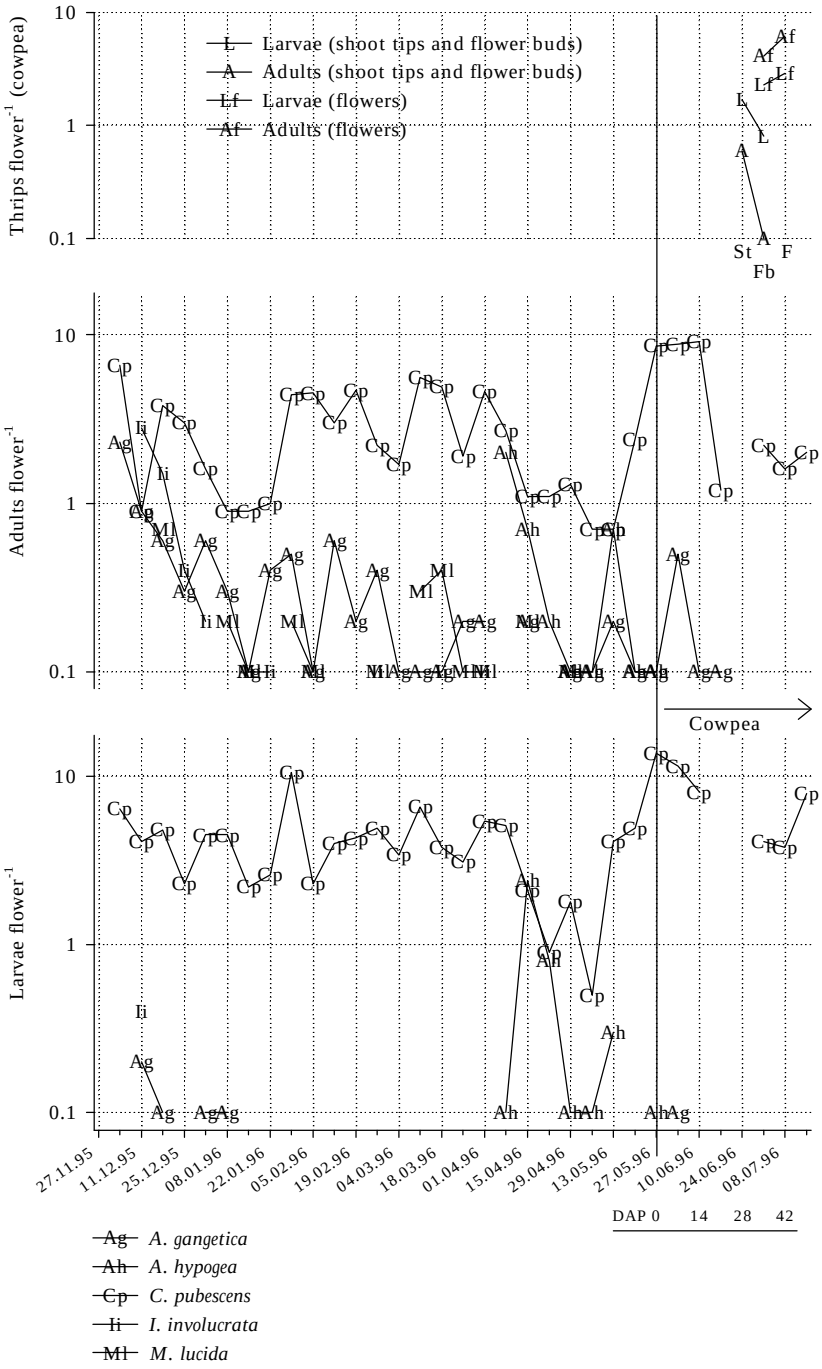
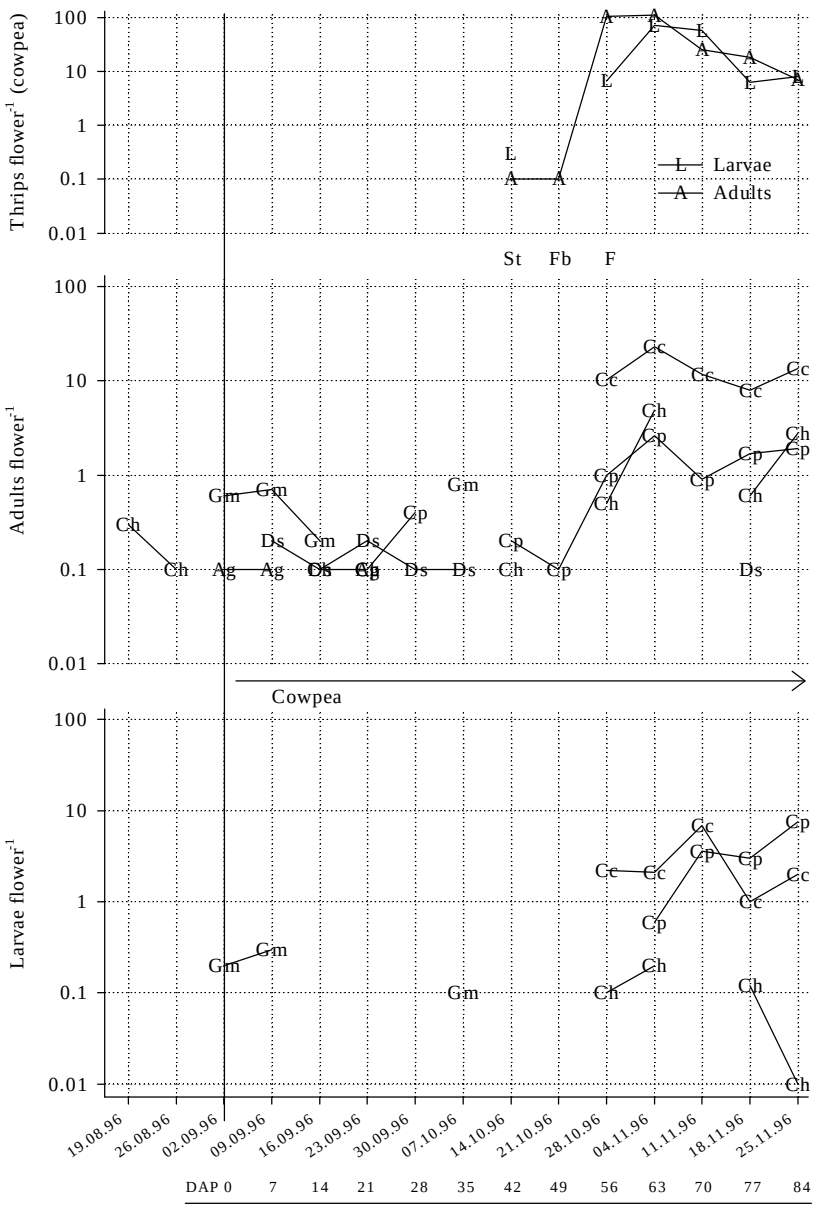


Fig. 7.5. Tokpa/Ayou, season II/96, population dynamics in alternative host plants, larvae and adults of *M. sjostedti* in cowpea compared with 6 species of alternative hosts. Values are means per flower, they were pooled across treatments for cowpea (larvae, adults), St = shoot tips, Fb = flower buds, F = flowers. The onset of cowpea cultivation is indicated by the respective DAP.



~~Ag~~ *A. gangetica*
~~Cc~~ *C. cajan*
~~Ch~~ *C. hirsuta*
~~Cp~~ *C. pubescens*
~~Ds~~ *D. saxatilis*
~~Gm~~ *G. max*

Fig. 7.6. Tokpa/Ayou, season I/97, population dynamics in alternative host plants, larvae and adults of *M. sjostedti* in cowpea compared with 7 species of alternative hosts. Values are means per flower, they were pooled across treatments for cowpea (larvae, adults), St = shoot tips, Fb = flower buds, F = flowers. The onset of cowpea cultivation is indicated by the respective DAP.

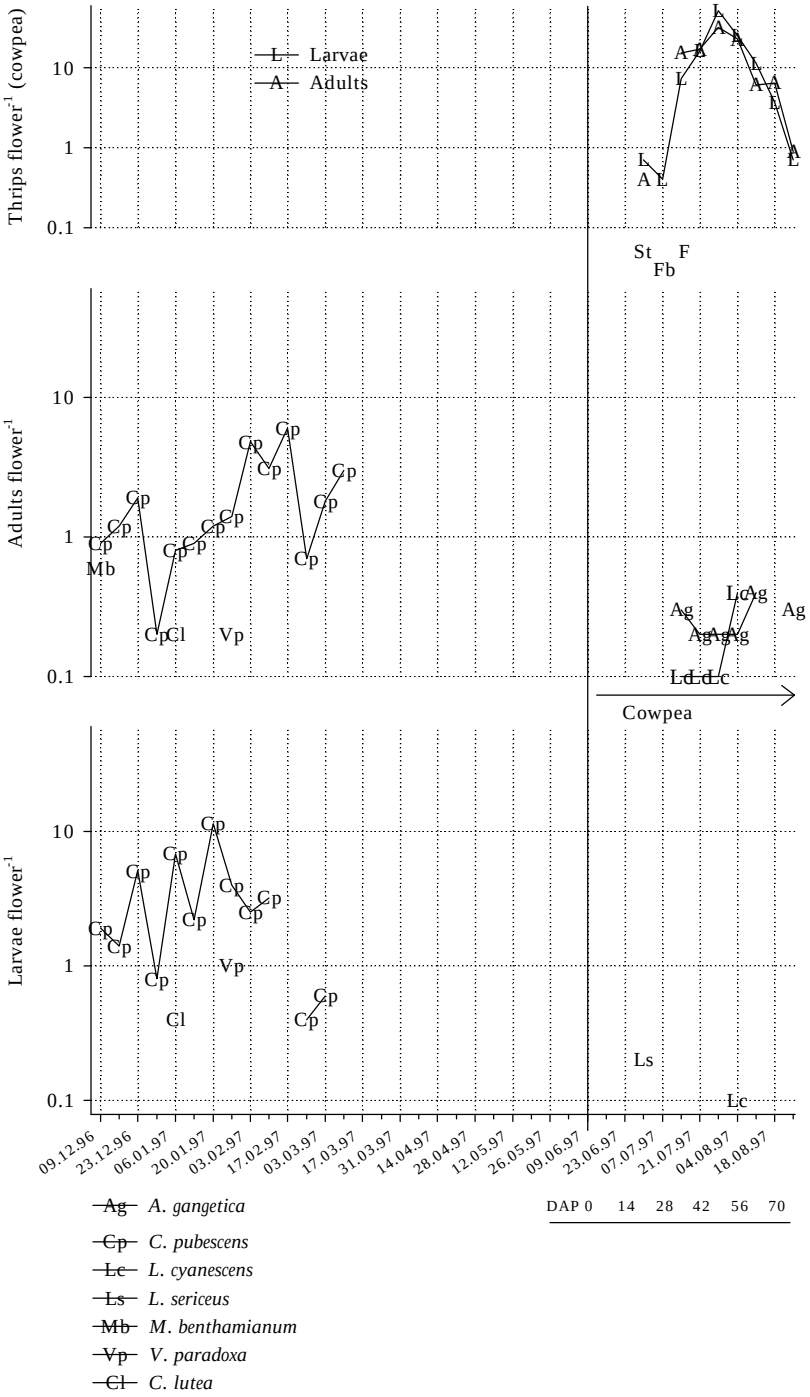


Fig. 7.7. Lema, season I/95, population dynamics in alternative host plants, larvae and adults of *M. sjostedti* in 2 species of alternative hosts. Values are means per flower. The onset of cowpea cultivation is indicated by the respective DAP. Sampling in cowpea was not started until Dap 42.

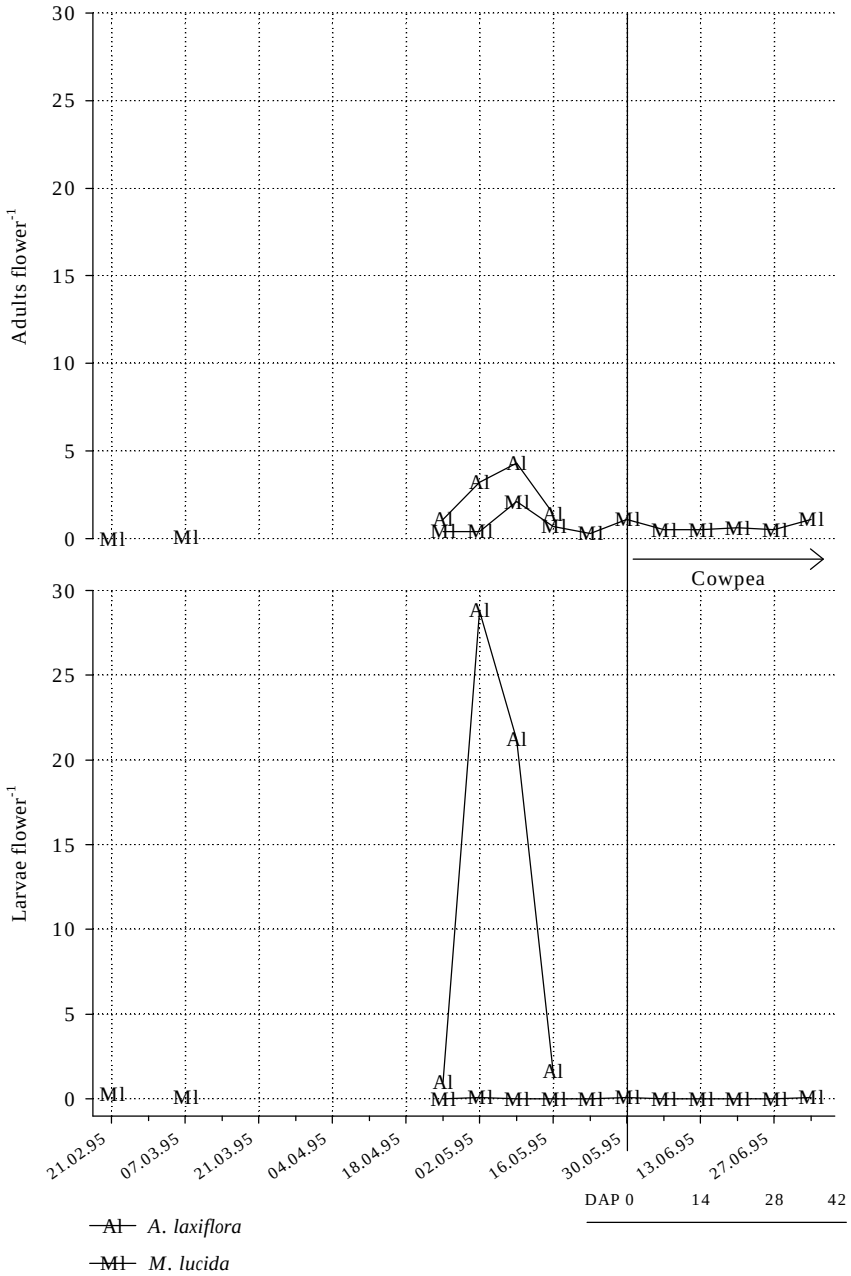


Fig. 7.8. Lema, season II/95, population dynamics in alternative host plants, larvae and adults of *M. sjostedti* in cowpea compared with 10 species of alternative hosts. Values are means per flower, St = shoot tips, Fb = flower buds, F = flowers. The onset of cowpea cultivation is indicated by the respective DAP.

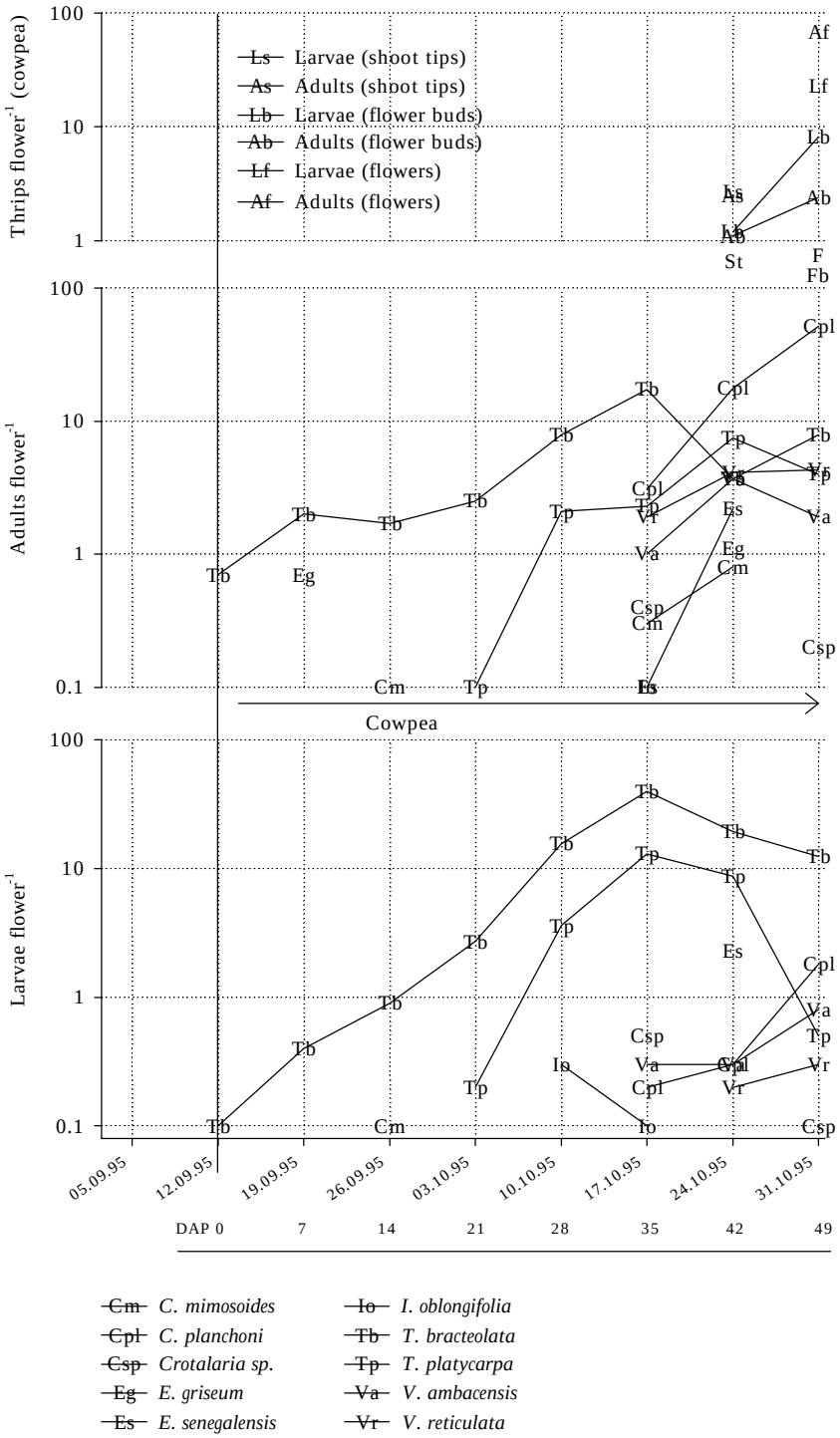


Fig. 7.9. Lema, season I/96, population dynamics in alternative host plants, larvae and adults of *M. sjostedti* in 6 species of alternative hosts. Values are means per flower. The onset of cowpea cultivation is indicated by the respective DAP.

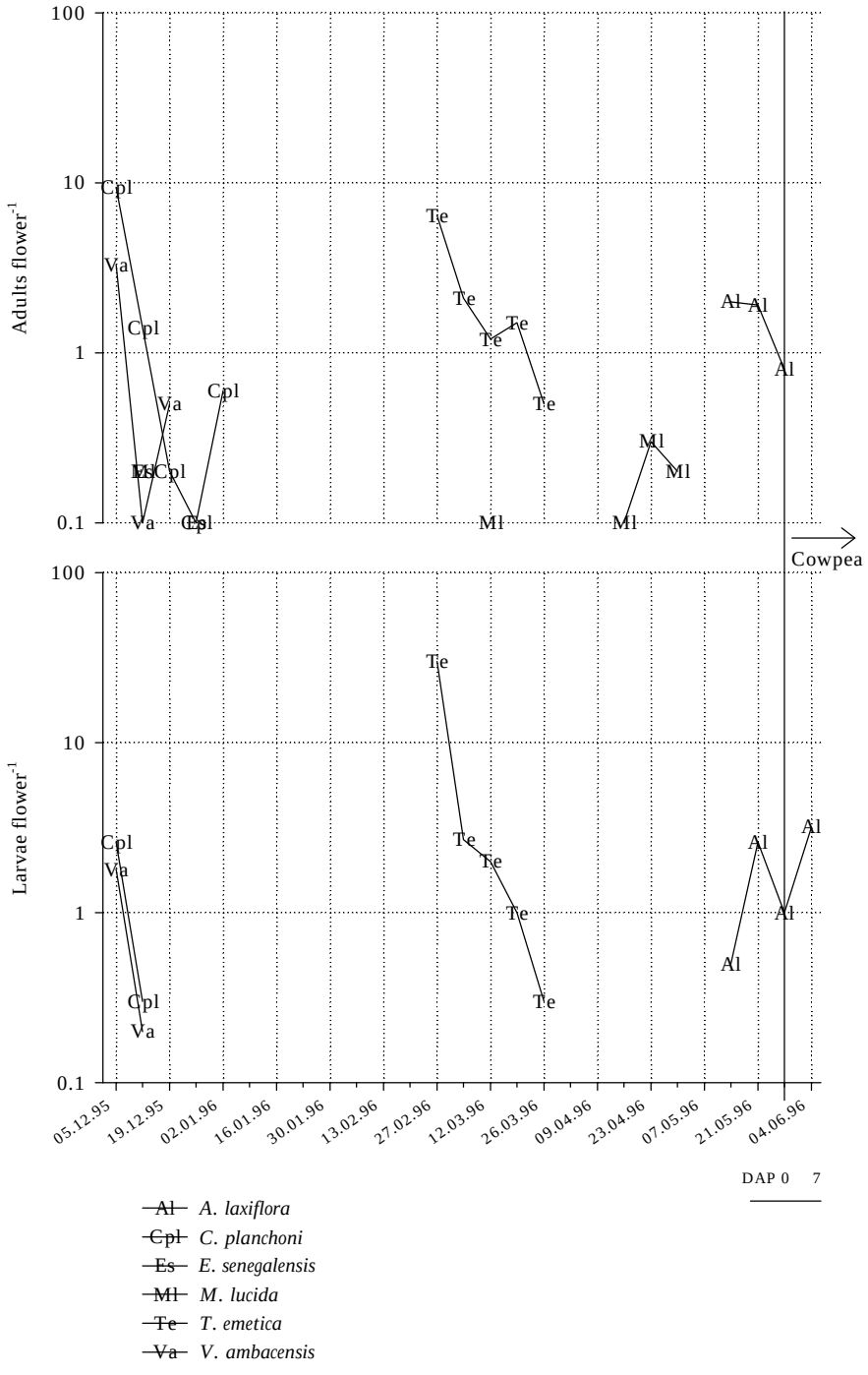


Fig. 7.10. Lema, season II/96, population dynamics in alternative host plants, larvae and adults of *M. sjostedti* in cowpea compared with 14 species of alternative hosts. Values are means per flower, St = shoot tips, Fb = flower buds, F = flowers. The onset of cowpea cultivation is indicated by the respective DAP.

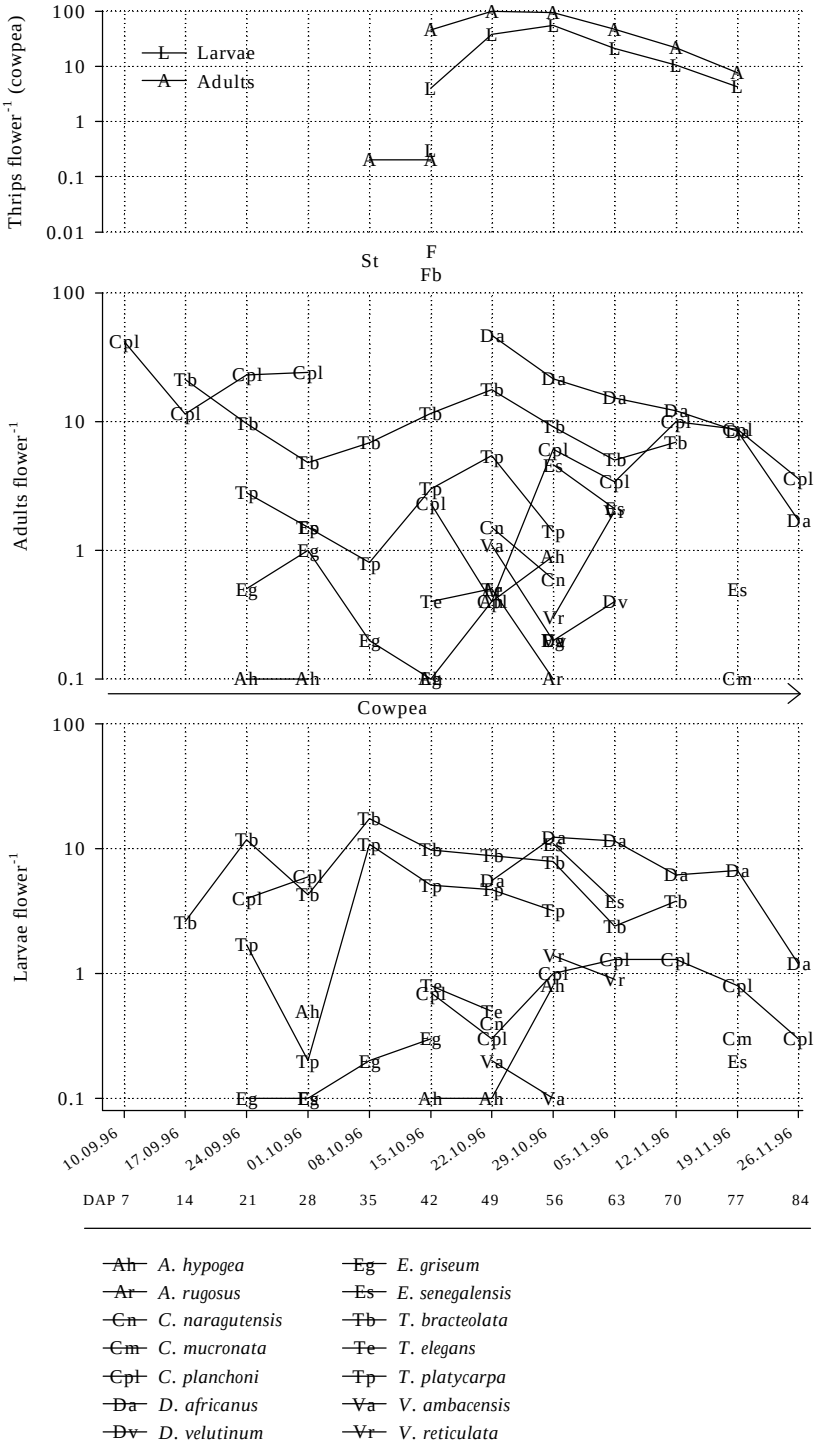


Fig. 7.11. Lema, season I/97, population dynamics in alternative host plants, larvae and adults of *M. sjostedti* in cowpea compared with 11 species of alternative hosts. Values are means per flower, St = shoot tips, Fb = flower buds, F = flowers. The onset of cowpea cultivation is indicated by the respective DAP.

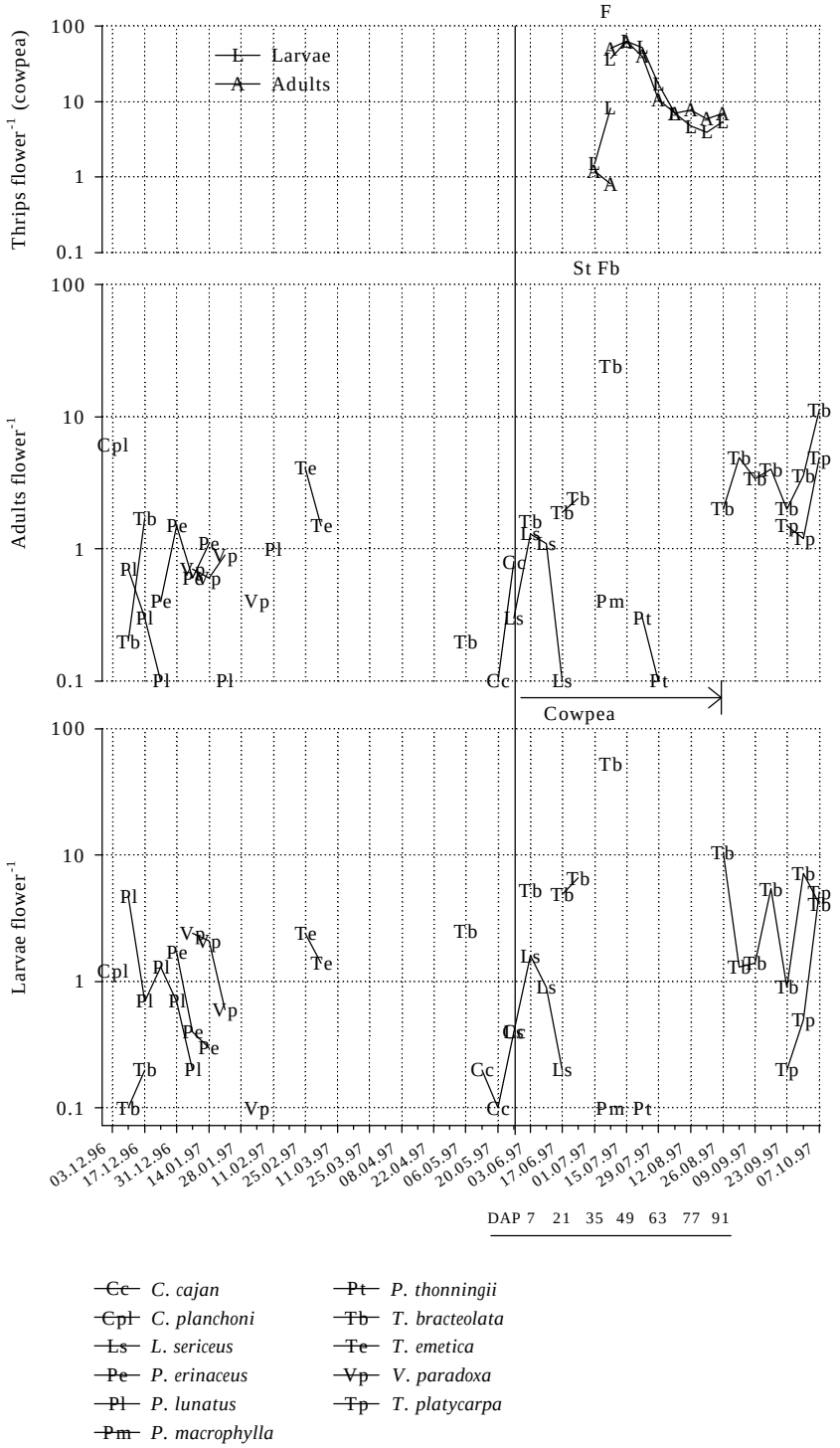


Fig. 7.12. IITA, season I/95, population dynamics in alternative host plants, larvae and adults of *M. sjostedti* in 3 species of alternative hosts. Values are means per flower. The onset of cowpea cultivation is indicated by the respective DAP.

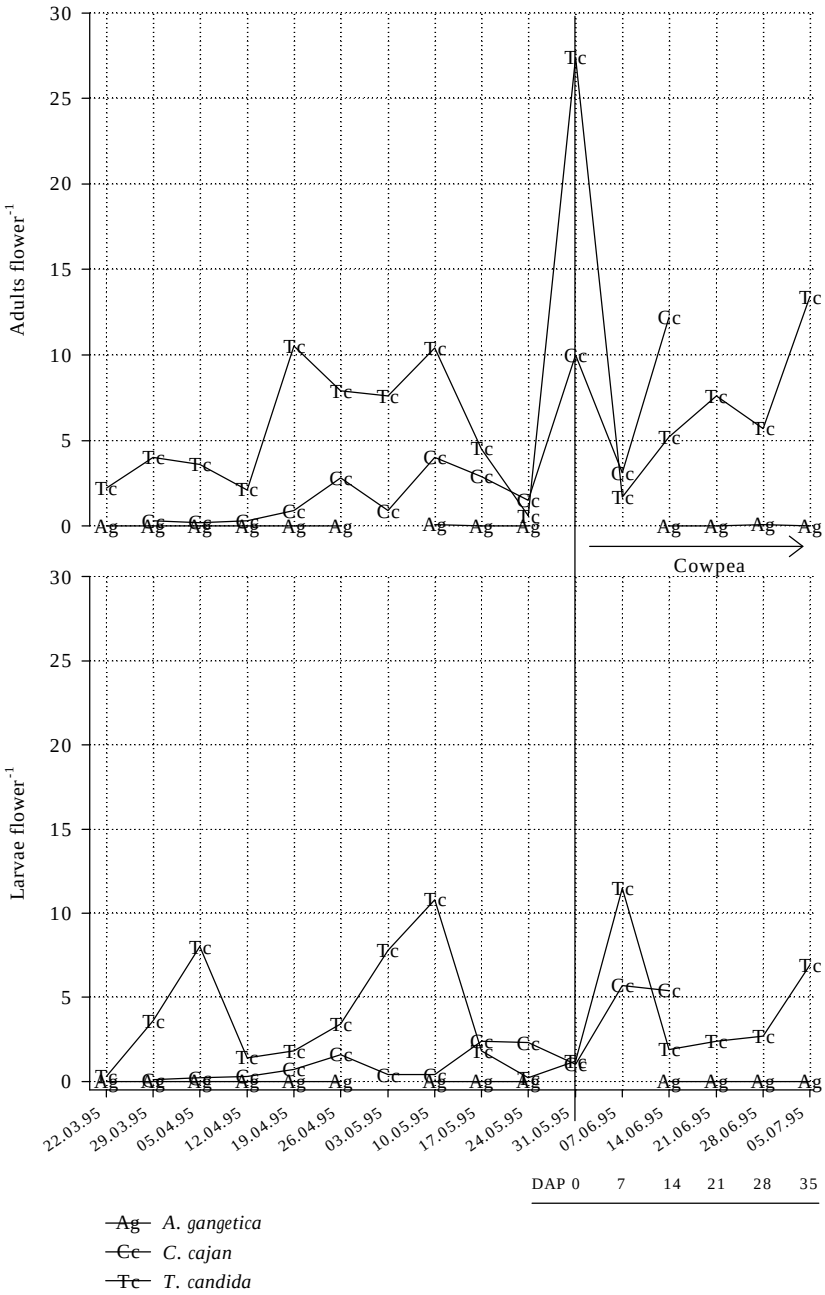


Fig. 7.13. IITA, season II/95, population dynamics in alternative host plants, larvae and adults of *M. sjostedti* in cowpea compared with 9 species of alternative hosts. Values are means per flower. The onset of cowpea cultivation is indicated by the respective DAP.

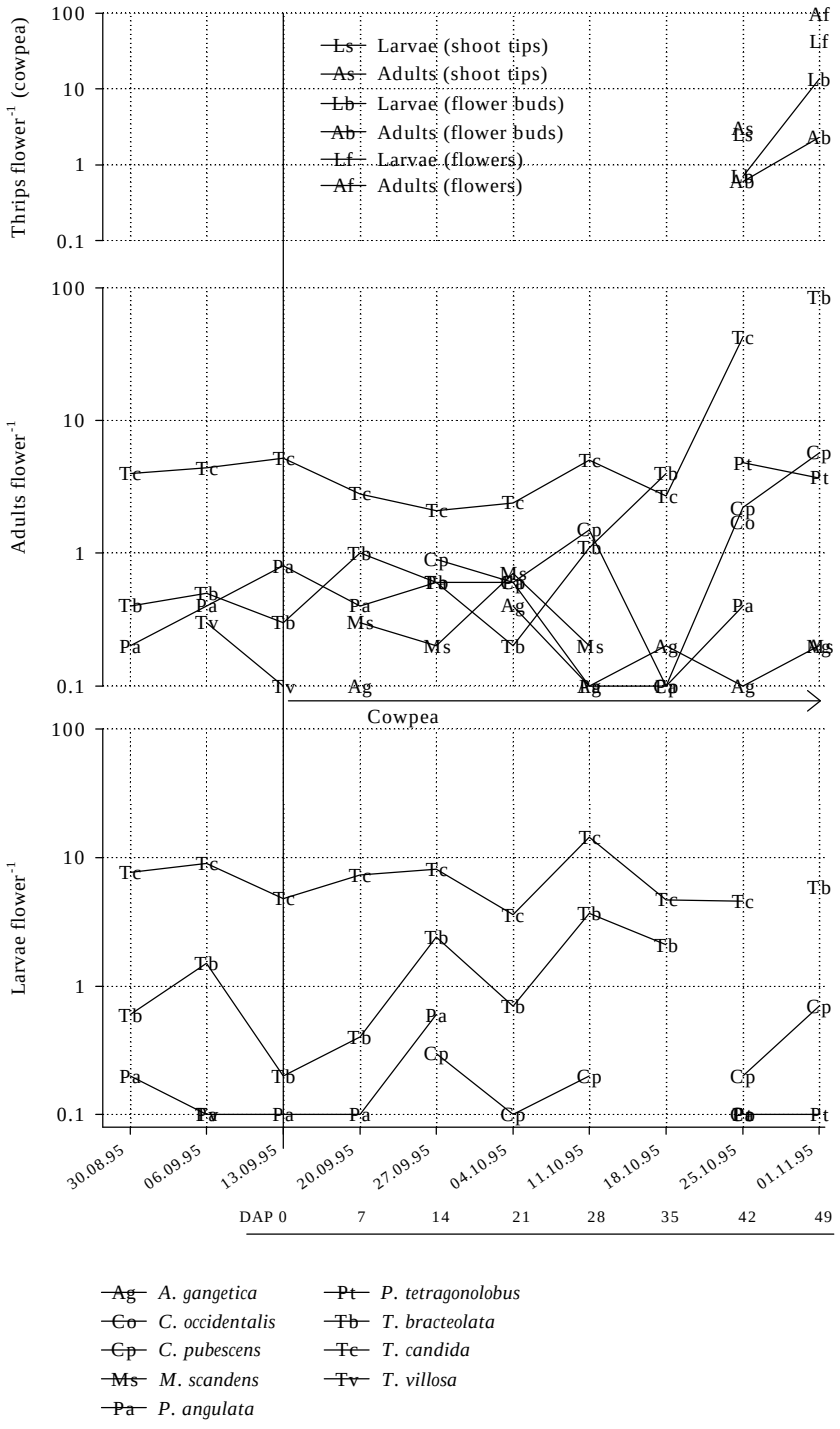


Fig. 7.14. IITA, season I/96, population dynamics in alternative host plants, larvae and adults of *M. sjostedti* in cowpea compared with 6 species of alternative hosts. Values are means per flower, St = shoot tips, Fb = flower buds. The onset of cowpea cultivation is indicated by the respective DAP.

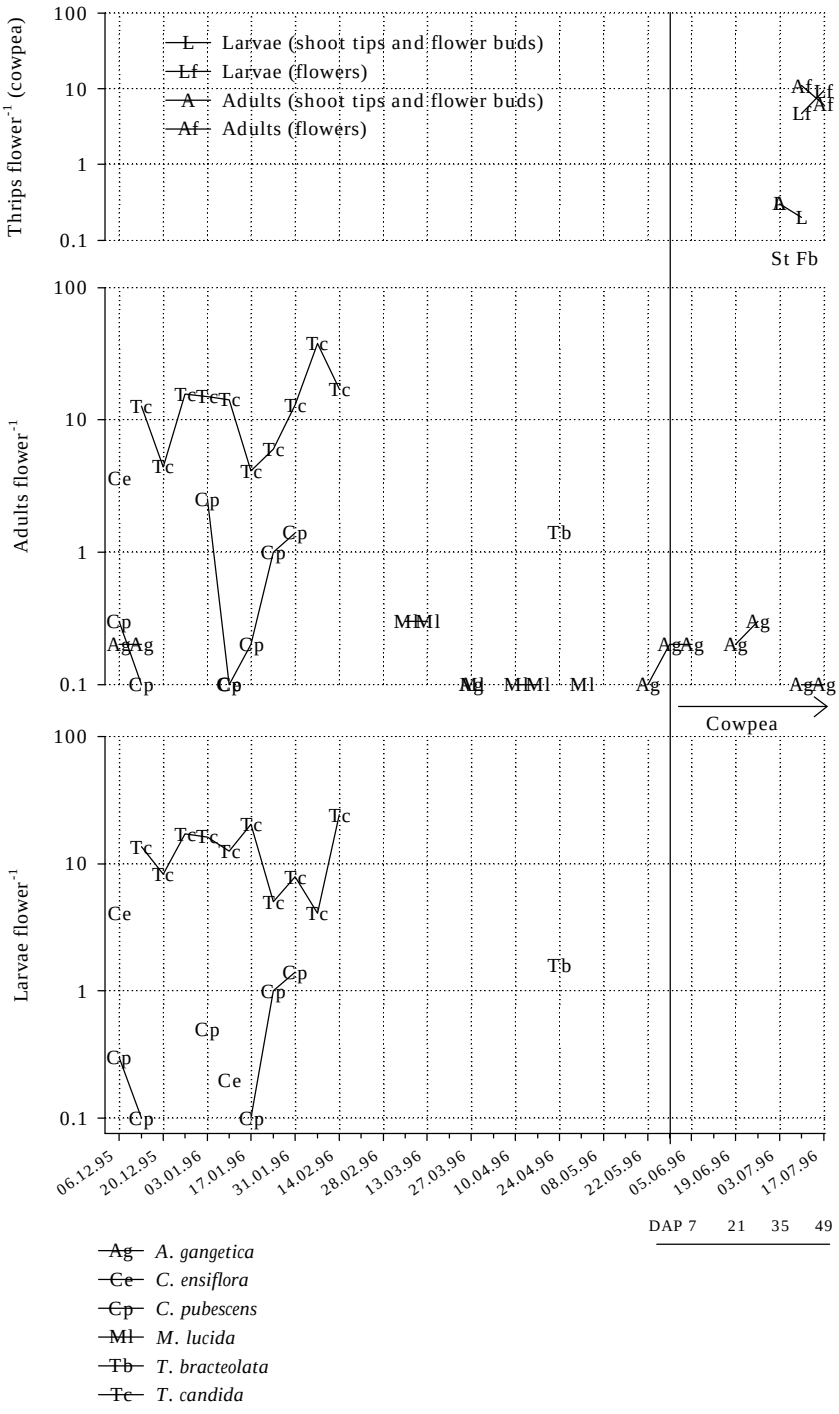


Fig. 7.15. IITA, season II/96, population dynamics in alternative host plants, larvae and adults of *M. sjostedti* in cowpea compared with 5 species of alternative hosts. Values are means per flower. The onset of cowpea cultivation is indicated by the respective DAP.

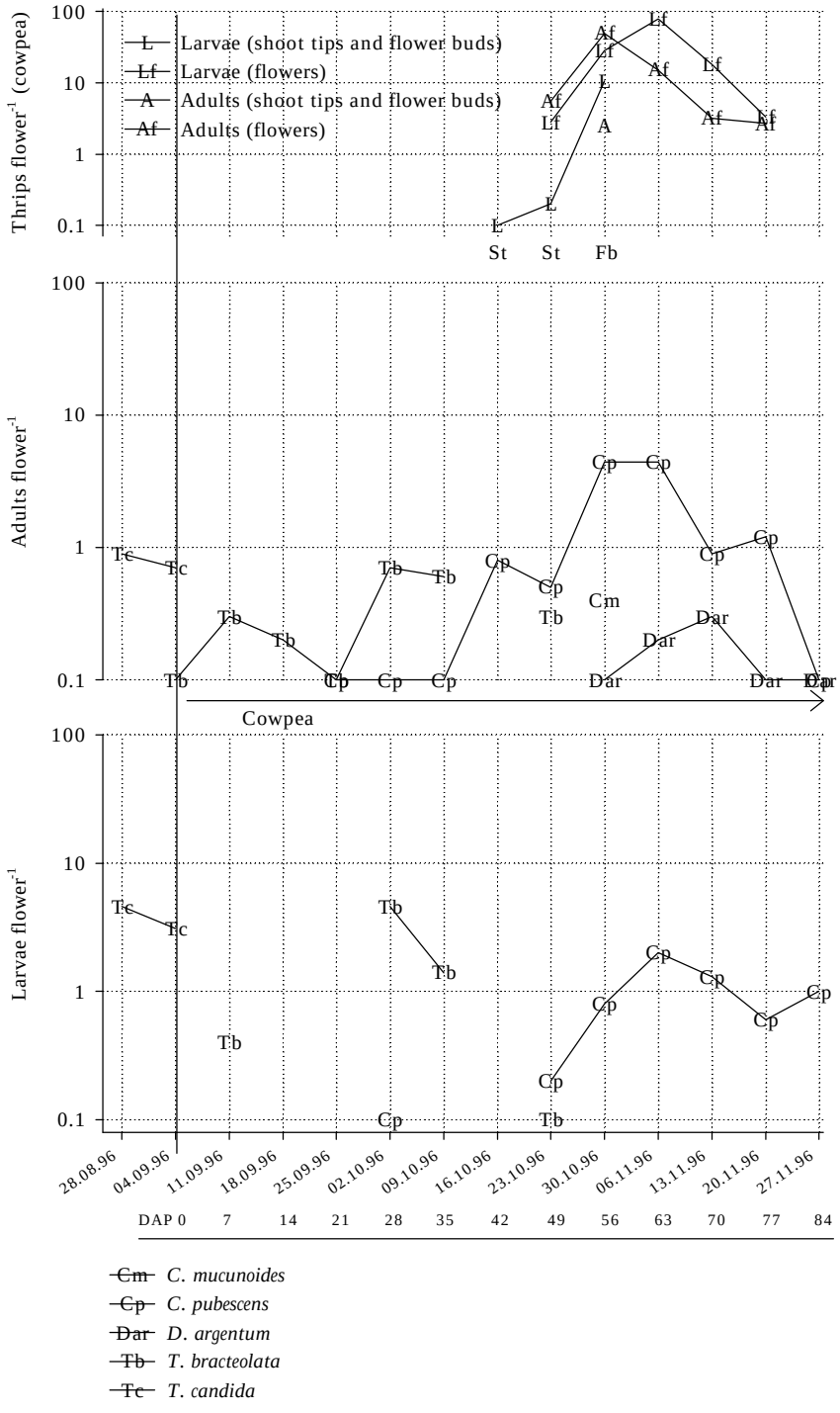
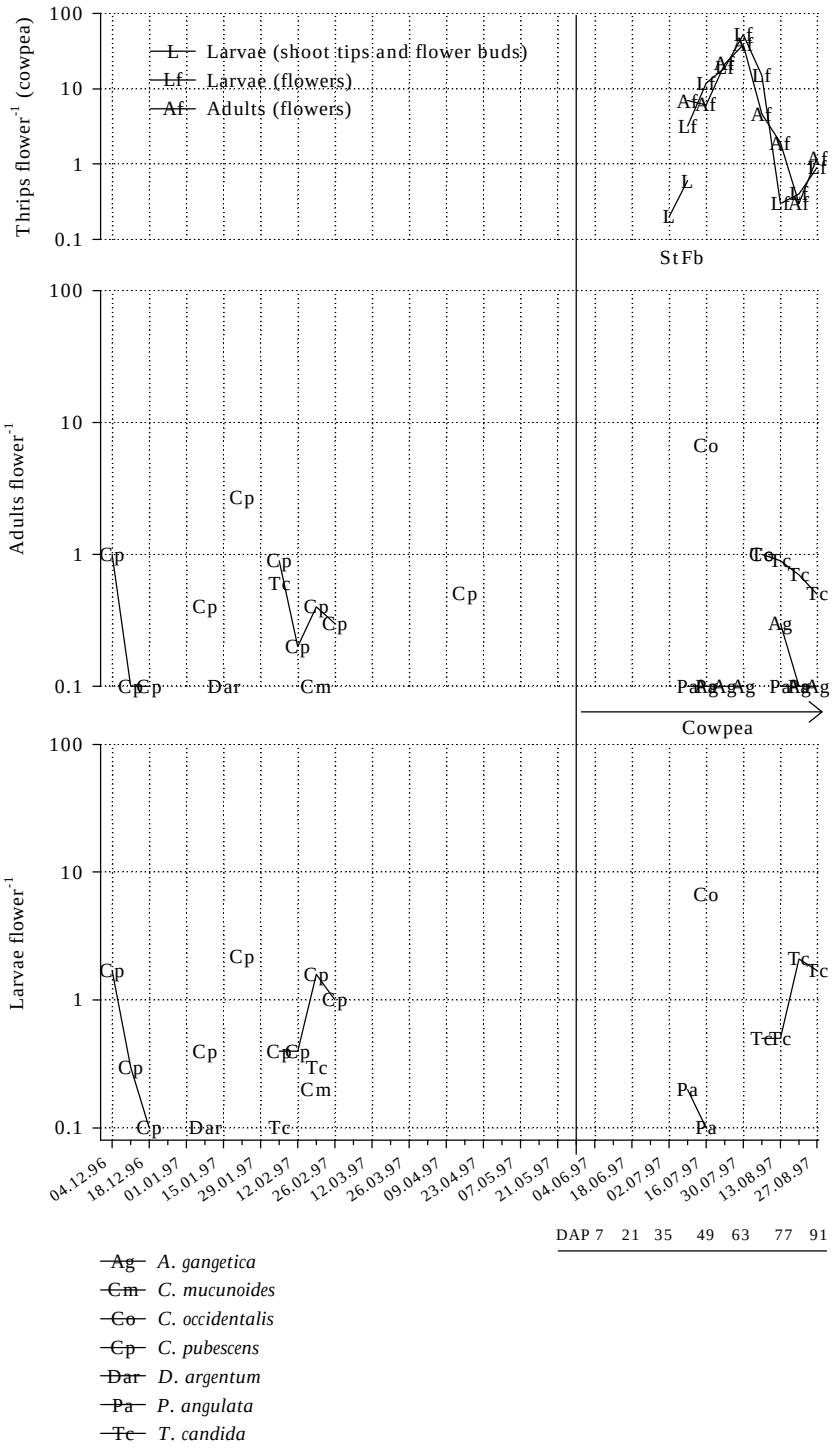


Fig. 7.16. IITA, season I/97, population dynamics in alternative host plants, larvae and adults of *M. sjostedti* in cowpea compared with 7 species of alternative hosts. Values are means per flower. The onset of cowpea cultivation is indicated by the respective DAP.



Appendix

Alternative host plants of *Maruca vitrata* and *Megalurothrips sjostedti* in the three different environments

All wild growing host plants that have been searched for are included in this list. Some of them have been found on some rare events only. The importance of these plants is judged on the number of organisms of *Maruca vitrata* and *Megalurothrips sjostedti* that were found in these environments. Reference to the list presented by Tamò (1991) reveals some differences in importance to pests, a fact that is mainly ascribed to the different locations where these wild host plants were sampled.

	Genus	Species	Familia	Location	Mar	Th	Sea
1	*Afrormosia*	*laxiflora*	Fabaceae	Le	-	●●●	I
2	*Alysicarpus**	*ovalifolius*	Fabaceae	Le	-	●	II
3	*Alysicarpus**	*rugosus*	Fabaceae	Le	-	●	II
4	*Asystasia*	*gangetica*	Fabaceae	I, To/Ay	-[1]	●	I, II
5	*Byrsocarpus**	*coccineus*	Fabaceae	To/Ay	-	●	I, II
6	*Cajanus*	*cajan*	Fabaceae	I, Le, To/Ay	●	●●[+]	I, II
7	*Calopogonium*	*mucunoides*	Fabaceae	I	-	●	I, II
8	*Canavalia*	*ensiflora*	Fabaceae	I	●	●	I
9	*Carpolobia*	*lutea*	Fabaceae	To/Ay	-	●	I
10	*Cassia*	*absus*	Caesalpiniaceae	Le	-	●	I, II
11	*Cassia*	*hirsuta*	Caesalpiniaceae	To/Ay	-	●	II
12	*Cassia*	*mimosoides*	Caesalpiniaceae	Le	-	●	II
13	*Cassia*	*occidentalis*	Caesalpiniaceae	I	-	●●	I, II
14	*Centrosema*	*pubescens*	Fabaceae	I, To/Ay	●	●●[+]	I, II
15	*Chromolaena**	*odorata*	Fabaceae	I, To/Ay	-	●	I, II
16	*Cochlospermum*	*planchoni*	Fabaceae	Le	-	●●●[+]	I, II
17	*Crotalaria*	*mucronata*	Fabaceae	Le	-	●	II
18	*Crotalaria*	*naragutensis*	Fabaceae	Le	-	●●	II
19	*Crotalaria*	*retusa*	Fabaceae	Le	-	-	I
20	*Crotalaria*	sp.	Fabaceae	Le	-	●	II
21	*Crotalaria**	sp.	Fabaceae	Le	-	●	II
22	*Dalbergia*	*saxatilis*	Fabaceae	To/Ay	-	●	II
23	*Desmodium*	*velutinum*	Fabaceae	Le	-	●	II
24	*Detarium*	sp.	Caesalpiniaceae	Le	-	-	I, II

25	*Dolichos*	*africanus*	Fabaceae	Le	●●$^{+}$	●●●$^{+}$	II
26	*Dolichos*	*argentum*	Fabaceae	I	-	●	I, II
27	*Eclipta**	*prostrata*	Asteraceae	I, Le, To/Ay	-	●	I
28	*Eriosema*	*griseum*	Fabaceae	Le	-	●$^{+}$	II
29	*Erythrinia*	*senegalensis*	Fabaceae	Le	●	●●$^{+}$	I, II
30	*Indigofera*	*oblongifolia*	Fabaceae	Le	-	●	II
31	*Indigofera*	sp.	Fabaceae	To/Ay	-	●	I
32	*Ipomoea*	*involucrata*	Convolvulaceae	To/Ay	-	●	I
33	*Lonchocarpus*	*sericeus*	Fabaceae	Le, To/Ay	●	●●$^{+}$	I
34	*Lonchocarpus*	*cyanescens*	Fabaceae	To/Ay	●$^{+}$	●$^{+}$	I
35	*Melanthera*	*scandens*	Asteraceae	I, To/Ay	-	●	II
36	*Mezoneuron*	*benthamianum*	Caesalpiniaceae	To/Ay	-	●	I
37	*Morinda*	*lucida*	Rubiaceae	I, Le, To/Ay	-	●	I, II
38	*Nauclea*	*latifolia*	Rubiaceae	Le	-	-	I
39	*Parinari*	sp.	Rosaceae	Le	-	-	I
40	*Parinari*	*macrophylla*	Rosaceae	Le	-	●	I
41	*Phaseolus*	*lunatus*	Fabaceae	Le	-	●●	I
42	*Physalis*	*angulata*	Solanaceae	I, To/Ay	-	●	I, II
43	*Piliostigma*	*thonningii*	Caesalpiniaceae	Le	-	●	I
44	*Psophocarpus*	*tetragonolobus*	Fabaceae	I	-	●	II
45	*Psydium*	*goyava*	Anacardiaceae	To/Ay	-	-	I
46	*Pterocarpus*	*erinaceus*	Fabaceae	Le	-	●●$^{+}$	I
47	*Rhynchosia*	*alba-pauli*	Fabaceae	Le	-	-	I
48	*Sida*	*rhombifolia*	Malvaceae	Le	-	-	II
49	*Stereospermum**	*kunthianum*	Bignoniaceae	Le	-	●	I
50	*Tephrosia*	*bracteolata*	Fabaceae	I, Le	●$^{+}$	●●●$^{+}$	I, II
51	*Tephrosia*	*candida*	Fabaceae	I	●	●●●$^{+}$	I, II
52	*Tephrosia*	*elegans*	Fabaceae	Le	-	●	II
53	*Tephrosia*	*platycarpa*	Fabaceae	Le	●$^{+}$	●●●$^{+}$	I, II
54	*Tephrosia*	*villosa*	Fabaceae	I	-	●	II
55	*Trichilia*	*emetica*	Meliaceae	Le	-	●●●	I
56	*Tridax**	*procumbens*	Asteraceae	I, Le, To/Ay	-	●	I, II
57	*Vigna*	*ambacensis*	Fabaceae	Le	●	●●	I, II
58	*Vigna*	*filicaulis*	Fabaceae	Le	-	-	II
59	*Vigna*	*reticulata*	Fabaceae	Le	●	●●	II
60	*Vitellaria*	*paradoxa*	Sapotaceae	Le	-	●●	I

I, Le, To/Ay — Respective site of occurrence: IITA (I), Lema (Le), Tokpa/Ayou (To/Ay).

Th — Importance of the plant as alternative host for *M. sjostedti* (Th)
- = not present, ● = little (0 > x ≤ 1 organism per flower), ●● = medium (1 > x ≤ 10), ●●● = very important (x > 10)

Mar — Importance of the plant as alternative host for *M. vitrata* (Mar)
- = not present, ● = little (0 > x ≤ 10 organism per 50 flowers), ●● = medium (x > 10)

Sea — Seasonal occurrence of wild growing host plants closely attached to the sampling periods during the early (I) and late (II) growing seasons.

* — Host plants where thrips larvae were never found but uniquely adults.

[1] — During the whole sampling period one larva was encountered.

[+] — Plants in which parasitized larvae of *M. vitrata* or *M. sjostedti* were encountered.

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Curriculum vitae

June 12, 1966	Birth at Schwenningen, South Germany
1972 to 1986	Primary and secondary School at Donaueschingen
October 01, 1986 to September 30, 1988	Duty in the German Navy in Eckernförde, Flensburg and Olpenitz/Schlei
October 15, 1988	Beginning of my studies in agricultural science at the University of Stuttgart-Hohenheim (Germany); option: Plant production
April 01, 1991 to September 30, 1991	Practice (required) on a family farm in Mosbach, north of Stuttgart (South Germany), 48 hectare
October 01, 1991 to March 31, 1992	Practice (voluntary) on the Estate "Fürst Thurn und Taxis“ at Hellkofen/Regensburg (South Germany), 600 hectare
April 15, 1992	Continuation of my studies at the University of Stuttgart-Hohenheim with the 6. Semester
August 10, 1992 to November 10, 1992	Guest student (hospitation program) in Ghana/West Africa in an extension project (GGAEP, Tamale) under the German Technical Co-operation (GTZ); Task: Investigation of the efficiency of the governmental extension service at the Ministry of Agriculture, Northern Region, Tamale (data collection for diploma thesis)
January 21, 1993 to February 24, 1993	Assistant (including responsibility for full documentation) during an international training course of the German Foundation for International Development (DSE) at Feldafing near Munich; Subject: "Extension in rural development" for graduate staff of African countries
October 15, 1993	9. semester; start of my thesis at the Institute of Agricultural Extension at the University of Stuttgart-Hohenheim; Subject: "Co-operation between agricultural research and agricultural extension - An empirical analysis in the Northern Region of Ghana"

January 07, 1994 to February 08, 1994	Co-moderation (including responsibility for full documentation) during an international training course of the German Foundation for International Development (DSE) at Feldafing near Munich; Subject: "Extension in rural development" for graduate staff of African and Asian countries
August 29, 1994	Completion of my studies with the degree diploma (agricultural engineer)
September 01, 1994	Start with my doctoral thesis in the Department of Applied Entomology of the Institute of Phytomedicine (Prof. Dr. C. P. W. Zebitz), University of Hohenheim; member of the Special Research Program (SFB) for West Africa, funded by the Deutsche Forschungsgemeinschaft (DFG)
October 15, 1994 to October 9, 1998	Data collection as well as analysis in the Republic of Benin, West Africa, in the "Plant Health Management Division" (PHMD) of the International Institute of Tropical Agriculture (IITA), Cotonou (Technical supervisor: Dr. Manuele Tamò); Topic: Research on biological control of insect pests in cowpea *(Vigna unguiculata* (L.) Walp.) with special regard to two major pests, the legume pod borer (*Maruca vitrata* F.) and the flower thrips (*Megalurothrips sjostedti* Trybom), as well as their antagonists
October 10, 1998 until present	Invitation to the International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya; finalization of the Ph.D. thesis and preparation for a position as postdoctoral fellow in the program “The African Fruit Fly Initiative,” headed by Dr. S. A. Lux. Subject: Behavioral ecology of three dipteran species (Ceratitis sp.) in cultivated and wild host plants

Nairobi, 03 February 1999

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Erklärung

Ich versichere, daß ich die vorliegende Dissertation selbständig angefertigt habe, nur die angegebenen Quellen und Hilfsmittel benutzt und wörtlich oder inhaltlich übernommene Stellen als solche gekennzeichnet habe.

Nikolaus Zenz

Nairobi, 03.02.1999