Aus dem Institut für
Pflanzenzüchtung, Saatgutforschung und Populationsgenetik
der Universität Hohenheim
Fachgebiet: Populationsgenetik

Prof. Dr. H.H. Geiger

Optimizing the development of seed-parent lines in hybrid rye breeding

Dissertation
zur Erlangung des Grades eines Doktors
der Agrarwissenschaften
Fakultät III – Agrarwissenschaften I –
Pflanzenproduktion und Landschaftsökologie
der Universität Hohenheim

von
Dipl.-Ing. agr.
Alexandra-Maria Tomerius
aus Wolfenbüttel

2001

Die vorliegende Arbeit wurde am 08.02.2001 von der Fakultät III – Agrarwissenschaften I – (Pflanzenproduktion und Landschaftsökologie) der Universität Hohenheim als "Dissertation zur Erlangung des Grades eines Doktors der Agrarwissenschaften" angenommen.

Tag der mündlichen Prüfung: 09.03.2001

Dekan:	Prof. Dr. K. Stahr
Berichterstatter, 1. Prüfer:	Prof. Dr. H.H. Geiger
Mitberichterstatter, 2. Prüfer:	Prof. Dr. W.E. Weber
3. Prüfer:	PD Dr. H.-P. Piepho

Table of contents

1 Introduction

1.1 Hybrid breeding in rye

Cross-pollinated populations consist of a wide array of heterozygous individuals. The basic idea of hybrid breeding is to identify and identically reproduce the best genotype(s) available in a population. This is achieved by the development of maternal and paternal components, usually inbred lines, and their controlled crossing resulting in a hybrid. To make maximum use of heterosis, the parental components are developed from genetically divergent gene pools. Hybrid varieties show a superiority in grain yield and other traits displaying heterosis, and are more uniform than open-pollinated varieties. Both properties make hybrid varieties highly attractive for the grower.

The basic requirements for a hybrid breeding program in a cross-fertilizing species are (i) self-fertility to allow the development of parental inbred lines, (ii) genetically divergent, well matching heterotic gene pools, and (iii) a reliable hybrid mechanism to ensure complete cross-pollination in the production of hybrid seed (Wricke and Weber, 1986).

In rye (*Secale cereale* L.), self-pollination is usually prevented by an effective gametophytic self-incompatibility system (Lundqvist, 1956; Voylokov, 1993). The detection of self-fertile forms (Wricke, 1973; Geiger, 1975), however, enabled the rapid development of inbred lines by continuous selfing. Systematic search for a suitable heterotic pattern revealed that the two widely used germplasm groups 'Petkus' and 'Carsten' were particularly well matching (Hepting, 1978). The Petkus pool is characterized by a high tolerance to abiotic stresses, superior plant density, and big kernels. Carsten materials excel by a high number of kernels per spike. The hybridizing mechanism employed for hybrid breeding and seed production in rye is a cytoplasmatic-genic male sterility (CMS) system detected by Geiger and Schnell (1970). CMS is based on the interaction of cytoplasmic factors causing male sterility with nuclear genes that either maintain pollen sterility (recessive alleles) or restore pollen fertility (dominant alleles). In a hybrid breeding program employing CMS, all seed-parent lines have to be maintainer genotypes. They must exist in two analogous forms, i.e. in normal (N) and in CMS-inducing cytoplasm, as the fertile N-form is needed to multiply the CMS-form. Pollen fertility in commercial hybrid seed and in testcross progenies is restored by nuclear genes of the pollinator parents. A detailed description of commercial hybrid-seed production in rye is given by Wortmann (1985).

Any plant breeding program consists of three major phases (Schnell, 1982): (i) the creation of initial genetic variability, (ii) the production and evaluation of parental components, and (iii) the production and evaluation of experimental varieties. A strongly simplified flow chart of hybrid rye breeding is given in Figure 1.1. Seed-parent and pollinator lines are developed from the two basic gene pools 'Petkus' resp. 'Carsten' to make maximum use of heterosis. Both base populations are reciprocally improved by recurrent selection (RS) and recycling of elite inbred lines to continually increase the chances of identifying superior hybrids (Sprague and Eberhart, 1977). As a first step in line development, the candidates *per se* are improved for traits that show a high heritability as well as a strong correlation between line and testcross performance like plant height, thousand-kernel weight, and resistance to lodging, pre-harvest sprouting, and various diseases. Thereafter, testcrosses to the respective opposite gene pool are produced by means of CMS, and testcross performance is assessed in multi-environmental trials. Selection at this stage is mainly for grain yield. Finally, experimental hybrids of the most promising candidates are developed. A nonrestorer single cross is used as seed-parent in producing experimental hybrids as well as commercial hybrid seed to obtain high yields of hybrid seed with good germination vigour. A narrow restorer synthetic consisting of two to four partially inbred lines is usually employed as pollinator.

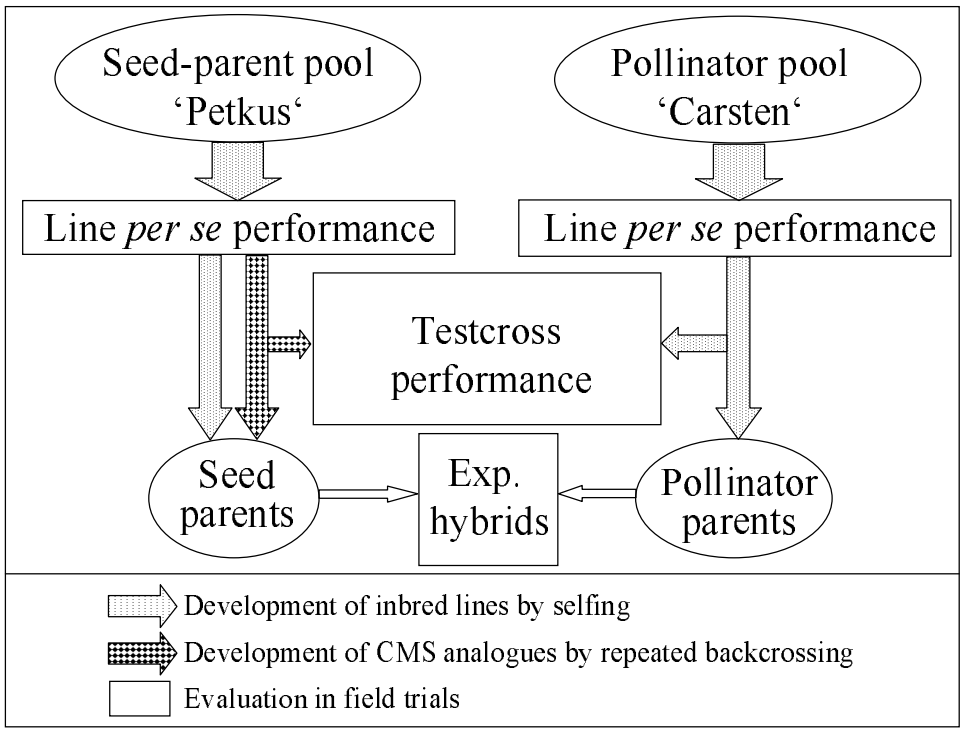

Fig. 1.1. Simplified flow chart of hybrid rye breeding

The importance of hybrid rye has steadily increased since the release of the first hybrid varieties in Germany in 1984 (Geiger and Miedaner, 1999). Currently, hybrids are grown on more than 60 % of the German rye acreage. In 2000, seventeen hybrid varieties were registered on the German variety list (Bundessortenamt, 2000), some of which are also registered and widely spread in other European countries (Madej, 1996). Hybrid breeding programs are also running in the two most important rye growing countries, Russia and Poland, and have recently been initiated in Belorussia and in Australia (Geiger and Miedaner, 1999). The yield superiority of hybrid rye has been proven in the official trials of many European countries (Madej, 1996). In the German official trials during 1982-1999, the three best hybrids outyielded the best open-pollinated entry by 1.03 t ha^{-1} (= 15.2 %) on average (Fig. 1.2). The yield superiority of hybrid varieties is increasing in spite of the intense efforts in population breeding. Progress has also been made for other important breeding goals such as lodging and sprouting resistance, bread making quality, and disease resistances (Geiger and Miedaner, 1999).

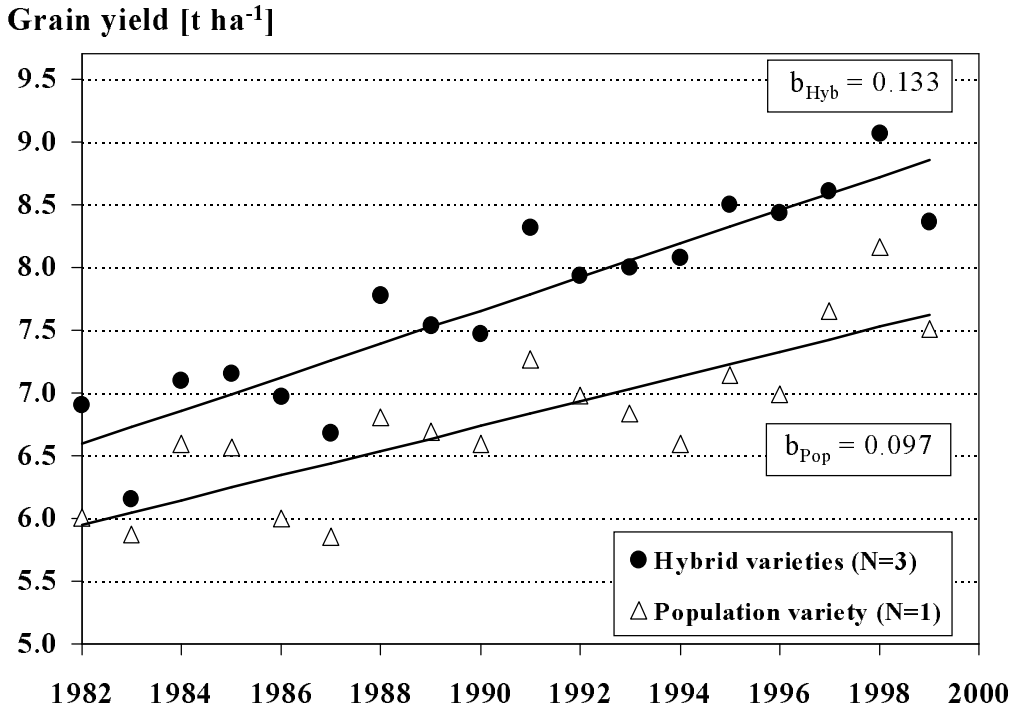

Fig. 1.2. Increase of grain yield of the best hybrid varieties compared to the best population variety in the German official trials during 1982-1999 (adapted from Geiger and Miedaner, 1999; Data from 'Bundessortenamt')

Presently used breeding schemes for the development of inbred lines in hybrid rye breeding are based on the comprehensive proposals of Geiger (1982, 1985). They have evolved according to the knowledge and practical experiences gathered in the last twenty years.

Nevertheless, the optimization of current breeding schemes and the development of alternative breeding strategies remain a continuous challenge for every practical breeder.

1.2 Optimization and comparison of alternative breeding schemes

In planning a strategy aiming at the development of new, superior varieties, a breeder has to decide on the breeding scheme to be used as well as on the dimensioning of every breeding step involved (Schnell, 1996). The breeding scheme determines the type and temporal order of the individual breeding steps as well as the genetic units, e.g. lines or testcrosses, to be used. The employable resources can then be allotted to the breeding steps in various ways. As a result, a multitude of possible breeding procedures exist which may strongly differ in their efficiency. It is therefore of utmost importance for the breeder to identify the most efficient procedure(s) among the many possible variants.

A suitable criterion for judging the efficiency of a breeding procedure is the gain from selection per unit of time and costs. While the realized gain from selection can only be assessed *a posteriori* in selection experiments, the expected gain of a breeding procedure can be predicted by model calculations or simulation studies allowing an *a priori* judgement.

Experimental comparisons of alternative breeding schemes are expensive, time consuming, and laborious. For a fair comparison, each scheme has to be evaluated across the same range of environments and under comparable agricultural techniques. To consider the sampling variance of the realized selection gain, several cycles of selection or several independent population samples have to be studied. Consequently, selection experiments only allow to compare very few, rather simple breeding procedures. They become impracticable for the comparison of complete breeding schemes aiming at the development of new varieties and for finding the optimum allocation of breeding resources to a given scheme.

Despite these shortcomings, a remarkable number of comparative selection experiments have been conducted in maize (Sprague and Eberhart, 1977; Hallauer and Miranda, 1981; Stojsin and Kannenberg, 1994; Weyhrich *et al.*, 1998). In contrast, only a few such experiments were reported in rye. Klinger (1985) investigated the suitability of selection based on line *versus* testcross performance in generation S_1 to increase the combining ability to a given tester. Results were, however, inconsistent over the two different base populations used. Loock (1991) found no significant differences between alternative RS methods aiming at the improvement of pre-harvest sprouting resistance in rye.

Theoretical comparisons of alternative breeding schemes can be accomplished by means of simulation studies or model calculations.

Simulation studies are based on genotypic and phenotypic values generated in a stochastic process. The expected response to selection is estimated as the difference between the means of the original and the selected population averaged over many simulation runs (Fraser and Burnell, 1970). Simulation studies require a number of assumptions at the genome level. These include the number of chromosomes and loci involved, the linkages among the loci, the individual genetic and environmental effects, the respective interactions among genes as well as between genes and environmental factors, and the distributions of the various effects. Simulation studies are particularly suited to study the long-term consequences of alternative breeding procedures since the effects of selection on the gene pool composition and the population structure can be followed in detail. Moreover, it is possible to precisely assess the variance of the expected selection gain.

Model calculations predict the expected gain from selection using quantitative-genetic regression theory. Prediction is based on estimates of the relevant population parameters such as components of genetic, genotype x environment-interaction, and error variance, and genetic correlation coefficients. Model calculations therefore require reliable population parameter estimates. As these estimates are solely valid for a limited number of selection cycles, only the short- to medium-term response to selection can be studied. Model calculations are especially suited to investigate the various aspects of practical breeding since the underlying parameters refer to concrete breeding materials, environments and characters, and practical requirements and restrictions can easily be taken into consideration. However, they also require a number of assumptions to be made (see Section 2). Besides, it is difficult to assess the variance of the expected gain from selection.

Both approaches, simulation studies and model calculations, allow to determine the efficiency of alternative breeding schemes as well as to identify their respective optimum variant under different assumptions. Virtually any number of possible breeding procedures can be analyzed in this way.

To guarantee a fair and meaningful comparison, the optimization of breeding schemes should always be carried out under adequate restrictions (Geiger and Tomerius, 1997). First, the resources available to each method should be limited, preferably on a monetary basis or with respect to the input of labour and testing capacity. In optimizing RS methods, the decline of

genetic variance has to be kept comparable as well. Finally, only the respective optimum variants (those with the best possible allocation of available resources under the actual assumptions) of alternative breeding schemes should be compared.

Theoretical investigations so far have largely focused on the comparison of alternative RS methods in self-pollinated species (Utz, 1983; Strahwald, 1988; Vanselow, 1990; Gallais, 1993; Goldringer *et al.*, 1996, 1997) as well as in different cross-pollinated crops like maize (Choo and Kannenberg, 1979; St. Martin, 1986) or pearl millet (Schipprack, 1993).
In rye, Wricke (1976) found S_1-line selection to be superior to half-sib family selection for the improvement of grain yield across different degrees of dominance and gene frequencies. In this study, however, none of the above mentioned restrictions was applied. Moreover, the correlation between S_1-line performance *per se* and general combining ability was derived on the basis of a single-locus model which lead to unrealistically high values. In model calculations assuming a constant annual labour capacity as well as an equal decline of genetic variance, Wilde (1987) compared RS methods suited for self-fertile rye populations. Combined selection on the *per se* performance of S_1- and S_2-lines and on S_1-testcross performance proved most efficient to improve general combining ability for an index comprising plant height, lodging resistance, thousand-kernel weight, and grain yield. Using the same approach, Loock (1991) investigated the efficiency of alternative RS methods to improve pre-harvest sprouting resistance. S_1-line selection was superior to full-sib family selection as long as the correlation between line and testcross performance was assumed to be moderate to high. Practical experiments did not reveal significant differences between both methods, however (see above).

Only few theoretical studies have been reported that deal with the development of new varieties or varietal components. Investigations on selection in segregating generations of autogamous crops have been conducted using model calculations (Utz, 1982; Weber, 1984) and simulation studies (van Oeveren and Stam, 1992; Grüneberg, 1993). Vermeer (1991) presented a simple model to optimize single-stage selection in potato breeding. Obaidi *et al.* (1998) studied the influence of alternative selection intensities on family *per se* response in the early selfing generations of maize inbred line development. A comprehensive model calculation study regarding the joint optimization of recurrent population improvement and pollen-parent line development in hybrid sugar beet breeding was conducted by Borchardt (1995).

Model calculations were also employed to compare alternative strategies for the selection of pollen-parent lines in hybrid rye breeding (Wilde, 1996). In this study, calculations were restricted to the second phase of inbred line development, i.e. selection for combining ability. Grain yield was considered to be the only trait under selection. A three-stage breeding scheme using testcrosses of restorer S_2-lines resp. S_3-bulks to CMS single cross testers was optimized assuming three different budgets. Two different selection strategies were compared: (i) OPT, leading to the highest possible gain from selection, and (ii) PRE, accepting a five percent reduction in selection gain in favour of an increase in testing intensity. Optimum allocations of resources for OPT and PRE differ mainly at the first selection stage. Under OPT, a large number of initial testcrosses to only one tester is evaluated and selection intensity is very high. With strategy PRE, the number of candidates entering the selection procedure is less than 50 % compared to OPT and thus selection intensity is reduced. However, as two testers are used to assess combining ability, the technical risk is reduced and the precision of selection increased. This makes the author prefer the PRE allocation under practical conditions. In the same study, the use of testcrosses of doubled haploid lines (DHL) instead of S_2-testcrosses was investigated. Assuming no extra costs for DHL-production and ignoring the genotypic limitations for anther culture response existent in rye, the use of DHL seems highly promising. Under more realistic conditions, however, the advantage of DHL drastically decreases due to the high actual costs and low regeneration rate of anther culture.

1.3 Objectives of the present study

In this study, model calculations aiming at the optimization of seed-parent line development in hybrid rye breeding are presented. They include all steps of the breeding process from the first selfing generation to the final evaluation of combining ability. Aspects of creating initial genetic variability are not specifically addressed and the evaluation of the experimental hybrids is not part of the optimization. The model calculations shall provide answers to the following questions:

- Which presently used breeding scheme is best suited for the development of seed-parent lines?
- Could doubled haploid lines increase the overall gain from selection?
- Would the use of an alternative hybridizing mechanism increase the efficiency of seed-parent line development?

- How should the available resources be allotted to a given breeding scheme to maximize the gain from selection?
- How much do deviations from the optimum allocation reduce the maximum gain from selection?
- How do changes in the underlying economic or quantitative-genetic parameters influence the optimum allocation of resources and the relative efficiency of a breeding scheme?

2 Description of the model calculations

In the model calculations presented, alternative schemes of seed-parent line development are optimized and compared on the basis of their expected selection gain per year under the assumption of a fixed annual budget. This chapter describes the alternative breeding schemes studied, the calculation of the optimization criterion employed, and the assumptions and parameters underlying the model calculations. A brief description of the optimization procedure and an overview of the situations investigated are also given.

2.1 Breeding schemes studied

All breeding schemes analyzed are composed of two major phases: selection for line performance followed by selection for combining ability. In all cases, line development starts from a non-inbred S_0-population. The ultimate goal of all breeding schemes is to select the three best seed-parent lines. The final evaluation of experimental hybrids is not considered in the calculations.

The alternative breeding schemes differ in the basic genetic material assumed, in the type of test units as well as in the number of selection stages for line and testcross selection, and in the cycle length. In the following, the scheme considered as a standard will first be described in detail. Afterwards, the deviating characteristics of the other breeding schemes will be explained.

In the standard scheme (Fig. 2.1), selection for line performance is carried out as a one-stage procedure. The test units employed are S_2-lines that have been derived by selfing from the initial S_0-population. Evaluation takes place in single row plots. After selection for line performance, conversion of the selected candidates into their male sterile CMS analogues is started. The conversion is necessary to allow the production of sufficient amounts of testcross seed for the following evaluation of combining ability. It is achieved by crossing S_2-plants to a CMS donor genotype followed by repeated backcrossing concurrently to the selfing process. Testcross seed is produced by crossing the CMS analogues to one or more restorer tester(s). Selection for combining ability is carried out as a two-stage procedure. Evaluation takes place in drilled plots of about $5m^2$ size. At the first stage, topcross progenies of CMS analogues of S_4-lines in backcross generation BC_1 are evaluated. The second evaluation stage employs topcross progenies of CMS analogues of S_6-lines in generation BC_2. Parallel to this, the production of experimental hybrids is started. First, seed-parent single crosses between existing superior CMS seed-parent lines (so called 'A-lines') and the foregoing candidate lines (as male-fertile 'B-lines') are produced in small plastic greenhouses. Single crosses of those

candidates that remain after the final selection step are then used to produce experimental hybrids in isolation plots employing three present restorer synthetics as pollinators. At the same time, the new parental lines are multiplied in small plastic greenhouses. The line development cycle is completed in eleven years.

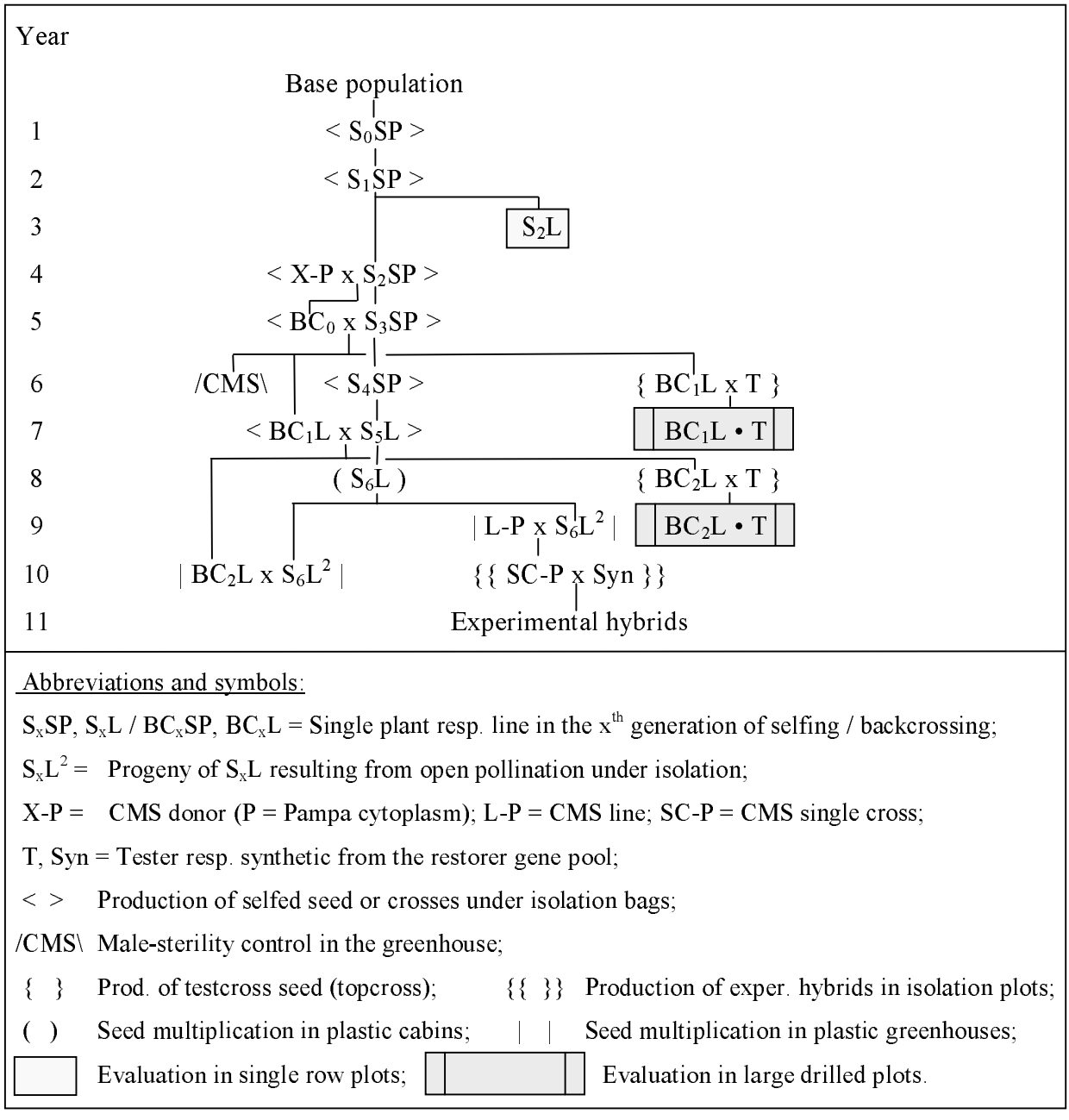

Fig. 2.1. Flow chart of the standard breeding scheme CYC1_11 (for explanation of the name see text below or Tab. 2.1)

The standard scheme described is especially suitable for genetic materials that have already undergone intense selection at the inbred and testcross level (second cycle material). For this type of material, breeding schemes are preferred in which the advancement of the candidate

lines is already carried out in parallel to the field trials that form the basis of selection among these lines (see Fig. 2.1). Once the selection decision is reached, only the selected lines are further used. In this way, the cycle length can be shortened, but at the cost of increased labour and expenses per candidate.

The breeding schemes investigated have been given names of the type 'AAAx_yz', in which 'AAA' denotes the basic type of the scheme and 'x_yz' denotes the number of selection stages to evaluate line performance (x) and testcross performance of the first (y) resp. second (z) type of testcross progeny. The standard scheme is thus called **CYC1_11** to indicate that the basic material employed is second **cyc**le material and that all types of test units are evaluated in **one**-stage procedures.

The first alternative breeding scheme analysed, **CYC1_21**, differs from the standard scheme only by an additional stage of testcross selection (Table 2.1; Fig. 7.1 in Appendix). In this scheme, the topcross progenies of the BC_1-lines are evaluated at two successive stages. Only those progenies that prove valuable at the first stage (pre-test) are further evaluated at the second stage (main test). Testcross performance of the BC_2-line testcross progenies is assessed at one stage as in CYC1_11. In total, evaluation of testcross performance is thus a three-stage procedure. Since an extra year is needed for pre-testing the BC_1-lines, the cycle length of CYC1_21 is prolonged to twelve years.

Table 2.1. Characteristics of the alternative breeding schemes studied (flow charts are given in Fig. 2.1 resp. in the Appendix (Fig. 7.1 – 7.4); for abbreviations see Fig. 2.1)

	Test units (No. of testing stages) employed to evaluate:				
Scheme[1]	Line performance		Testcross performance		Length [yrs.]
CYC1_11	S_2L (1)		$BC_1L \bullet T$ (1)	$BC_2L \bullet T$ (1)	11
CYC1_21	S_2L (1)		$BC_1L \bullet T$ (2)	$BC_2L \bullet T$ (1)	12
POP2_11	S_1L (1)	S_2L (1)	$BC_1L \bullet T$ (1)	$BC_2L \bullet T$ (1)	13
DHL1_11	DHL (1)		$BC_1L_{DH} \bullet T$ (1)	$BC_2L_{DH} \bullet T$ (1)	10
GAM1_11	S_2L (1)		$T \bullet S_2L$ (1)	$T \bullet S_4L$ (1)	9

[1] Names 'AAAx_yz' of the breeding schemes denote:
(i) AAA = type of the scheme: CYC = 2nd cycle scheme, POP = scheme for broader-based population material, DHL = doubled haploid line scheme, GAM = testcrosses produced by means of gametocides;
(ii) x_yz= no. of selection stages employed to evaluate line performance (x) and testcross performance (y, z = evaluation of 1st resp. 2nd type of testcross progeny).

Progress from second cycle breeding can only be expected as long as there is sufficient genetic variability for the traits under selection. Thus, a breeder cannot confine all efforts to this approach but must also devote work to broadening the genetic base of the breeding population by introducing alien materials. If the latter have not undergone several cycles of inbreeding and selection before, a much higher proportion of inferior candidates has to be expected due to a higher load of unfavourable recessive mutations. A breeding scheme to be used under these circumstances therefore has to differ from a second cycle scheme. In the model calculations, scheme **POP2_11** (Table 2.1; Fig. 7.2 in Appendix) is used to study the development of seed-parent lines from base-broadened populations. In this scheme, evaluation of line performance is carried out as a two-stage procedure employing S_1-lines and S_2-lines. Testcross evaluation corresponds to the standard scheme. The cycle of POP2_11 is two years longer than that of the standard scheme since advancing the lines by selfing and / or backcrossing needs to be postponed until a positive selection decision has been reached in S_1 and S_2 to avoid labour and expenses for candidates that are not worth being continued.

In many different crops, the use of doubled haploid lines (DHL) has increased the efficiency of breeding by (i) shortening the cycle length and (ii) allowing a better differentiation among the candidates. A breeding scheme employing DHL, **DHL1_11**, (Table 2.1; Fig. 7.3 in Appendix) is also investigated in this study. It is assumed that DHL are produced by means of anther culture. Since winter rye needs more than eight weeks of artificial vernalization, DHL development takes two years including seed multiplication (Flehinghaus-Roux, 1994). Line performance of the DHL can thus not be assessed before the third year. Afterwards, crossing with the CMS donor and production of the BC_1 are carried out in one year in the greenhouse. Selection for combining ability takes place as in the standard scheme. The BC_1-lines and BC_2-lines in this case are CMS analogues of the completely homozygous DHL, however. The cycle length of DHL1_11 is ten years.

The use of CMS as hybridizing mechanism renders the development of seed-parent lines in rye rather complicated and costly. Model calculations are therefore carried out to investigate the potential of employing an alternative hybridizing mechanism. The use of a gametocide instead of CMS is studied in scheme **GAM1_11** (Table 2.1; Fig. 7.4 in Appendix). As in the standard scheme, S_2-lines are evaluated for line performance. Afterwards, testcross evaluation is carried out at two successive stages. First, the selected S_2-lines are crossed as pollinators to one or more tester(s) from the opposite gene pool that have been treated with a gametocide. The candidate lines are used as pollinators because only remnant seed of the S_2-lines is available, but sufficient amounts of testcross seed are needed for the evaluation of combining

ability. Moreover, this approach increases the technical security of testcross-seed production since application date and dose of the gametocide can be optimized for the testers employed. Comparable testcrosses of S_4-lines are used at the second evaluation stage. It is assumed that the gametocide is only used for the production of testcrosses whereas commercial hybrid seed is still produced by means of CMS for economic reasons. The production of CMS analogues of the most promising candidates is started in parallel to the second stage of testcross evaluation. One cycle of GAM1_11 is completed in nine years.

2.2 Calculation of the optimization criterion

2.2.1 The expected gain from selection

In plant breeding, selection decisions are based on the observed performance of test units in evaluation trials. The selection criterion, x, is the performance mean across environments and replicates. The biometrical model for the mean of the i^{th} test unit is:

$$x_i = \mu + t_i + \frac{\Sigma p_j}{P} + \frac{\Sigma q_k}{Q} + \frac{\Sigma tp_{ij}}{P} + \frac{\Sigma tq_{ik}}{Q} + \frac{\Sigma pq_{jk}}{PQ} + \frac{\Sigma tpq_{ijk}}{PQ} + \frac{\Sigma r_{jkl}}{PQR} + \frac{\Sigma e_{ijkl}}{PQR}$$

where

μ	is the general mean,
t_i	the genotypic effect of the i^{th} test unit,
p_j, q_k, pq_{jk}	the effects of the j^{th} location, the k^{th} year, and the interaction between the j^{th} location and the k^{th} year, resp.,
tp_{ij}, tq_{ik}, tpq_{ijk}	the effects of the pertinent interactions with the i^{th} test unit,
r_{jkl}	the effect of the l^{th} replicate at the j^{th} location in the k^{th} year,
e_{ijkl}	the experimental error,
P, Q, R	the number of locations, years resp. replicates employed for the evaluation of the test units.

All effects except μ are assumed to be uncorrelated and normally distributed variables with mean zero and variances σ^2_t, σ^2_p, σ^2_q, σ^2_{pq}, σ^2_{tp}, σ^2_{tq}, σ^2_{tpq}, σ^2_r, and σ^2_e, respectively. According to the biometrical model, the phenotypic variance of the selection criterion is:

$$\sigma^2_x = \sigma^2_t + \frac{\sigma^2_{tp}}{P} + \frac{\sigma^2_{tq}}{Q} + \frac{\sigma^2_{tpq}}{PQ} + \frac{\sigma^2_e}{PQR}.$$

The gain criterion of selection, y, is the genetic superiority of the target units for the trait of interest. It can either relate to (i) the total genotypic value, (ii) the additive genetic value, or (iii) the combining ability of the target units.

The expected gain, G, from one-stage truncation selection can be predicted as

$$G = i\,\rho_{xy}\,\sigma_y \qquad \text{(Cochran, 1951)},$$

where i is the selection intensity, ρ_{xy} denotes the correlation coefficient between the selection criterion and the gain criterion, and σ_y is the genetic standard deviation of the gain criterion. The selection intensity is the phenotypic superiority of the selected test units expressed in phenotypic standard deviations. For a normally distributed selection criterion it depends on the size of the selected fraction only. In small samples, corrections based on order statistics become necessary (Burrows, 1972). The correlation between the selection and the gain criterion is determined by the genetic correlation between the test units and the target units, ρ_{ty}, and the square root of the heritability of the selection criterion: $\rho_{xy} = \rho_{ty}h_x$. This correlation can be strengthened by increasing the number of locations, years, and replicates and thus reducing the masking variation caused by genotype x environment-interaction and error effects. The genetic standard deviation of the gain criterion, σ_y, depends solely on the trait(s) under selection and the base population used.

In the breeding schemes studied, selection is carried out as a multi-stage procedure. After the first selection stage, the genetic variance in both the selection and the gain criterion is reduced among the remaining candidates compared to the initial population (Cochran, 1951). Moreover, the remaining genotypes are no longer normally distributed with respect to the gain criterion. The prediction formula for G given above is thus no longer valid. To predict the gain from multi-stage selection, the distribution of the candidates at each selection stage has to be known. Cochran (1951) derived exact formulae to predict the gain from two-stage selection and Utz (1969) extended his approach to three-stage selection. The formulae and computations are described in detail in the Appendix (Section 7.2). Apart from the standard deviation of the gain criterion, the gain from multi-stage selection depends on (i) the fractions selected at the individual selection stages, (ii) the correlations between the selection criterion used at each stage and the gain criterion, and (iii) the correlations between the selection criteria employed at the different selection stages.

2.2.2 Selection, gain, and optimization criterion in the model calculations

For the model calculations the breeding schemes are subdivided into two successive phases: selection for line performance and selection for combining ability (see Table 2.1, Fig. 2.1).

In a breeding program, the breeder usually aims to improve a number of traits simultaneously. Thus, a selection index $I = \Sigma_i b_i x_i$ is employed as selection criterion in the model calculations, where b_i and x_i are the index weight resp. the phenotypic mean of the test unit for trait i (Wricke and Weber, 1986). The selection index for line performance comprises plant height, lodging resistance, thousand-kernel weight, falling number, and leaf rust resistance. It is assumed that the genotypic effects of all traits in the index are uncorrelated. The index weights b_i are calculated as the product of the economic weight of trait i, a_i, and the narrow sense heritability of the test unit in trait i (Baker, 1986). The gain criterion is the total economic value $H = \Sigma_i a_i y_i$ of the target units, where y_i is the genotypic effect of the target unit regarding trait i. In seed-parent line development the target units are random homozygous inbred lines derived from the selected candidates.

The index employed to select for combining ability comprises the above mentioned traits plus grain yield as the most important trait. Again, the genotypic effects of all traits in the index are assumed to be uncorrelated. Though the two successive selection phases are treated separately, the reduction of the genotypic variance for combining ability among the candidates that is caused by the preceding selection for line performance is taken into account. Due to the uncorrelatedness of the traits it is assumed that the genetic variance for grain yield remains unaffected by selection for line performance. The reduced genetic variances in the selection and the gain criterion for the other traits are calculated using a modification of the formula given by Cochran (1951). In this modified formula, the variance reduction is multiplied by the coefficient of the genetic correlation between line performance and testcross performance because otherwise an overadjustment would result.

Concerning selection for combining ability it is assumed that the breeder is mainly interested in seed-parent lines that match the total pollinator gene pool and not only specific genotypes out of it. The gain criterion in this phase is thus the total economic value of the target unit regarding general combining ability (GCA).

The breeding schemes studied are first optimized *per se*. To obtain the optimization criterion, the expected standardized selection gains per year in the total economic value regarding line performance resp. regarding GCA are first calculated separately using the formulae of Utz (1969; see Section 7.2) and the parameter estimates given in the following chapter. Only the direct selection gains are considered. These two values are then summed up weighing the gain in line performance resp. in GCA in the ratio of 1 : 3 to reflect the fact that the improvement of GCA is of primary interest in hybrid breeding.

For the comparison of the alternative variants of the schemes, the standard deviation of the gain criterion has to be taken into account in order to reflect the actual gains in the traits under selection. Thus the criterion used to compare and valuate the schemes is the weighed sum of the non-standardized yearly selection gains in line performance resp. in GCA.

2.3 Model assumptions and parameters

2.3.1 Quantitative-genetic parameters

In the model calculations it is assumed that the S_0 base population is in gametic phase equilibrium prior to selection and that epistatic and reciprocal effects are absent. The genetic variance among test units, σ^2_t, is expressed as a linear function of the additive and dominance variance, σ^2_A resp. σ^2_D, in the base population as follows:

The genetic variance among testcross progenies is

$$\sigma^2_t = \sigma^2_{GCA} + \frac{\sigma^2_{SCA}}{T} \qquad \text{(Griffing, 1956),}$$

where σ^2_{GCA} is the GCA variance of the candidate lines, σ^2_{SCA} the specific combining ability (SCA) variance, and T the number of testers used. The expectations of the GCA variance of the candidates and the SCA variance in terms of σ^2_A and σ^2_D are:

$\sigma^2_{GCA} = 0.5 \varnothing \sigma^2_A$,

$\sigma^2_{SCA} = \varnothing \varnothing_T \sigma^2_D$ (Kempthorne, 1957).

In these formulae, $\varnothing$ and $\varnothing_T$ denote the probability that two random individuals of a given testcross progeny have received alleles identical by descent from the candidate line resp. the tester. Since many individuals of each candidate line and of the tester are employed in producing the testcross seed, $\varnothing$ and $\varnothing_T$ equal the coefficient of coancestry, f, between two random individuals of the candidate line resp. of the tester. The coefficient of coancestry is equal to (i) the inbreeding coefficient F_t in case of an inbred line, (ii) 0.5 for a single-cross tester, and (iii) $(1+F_x) / 2n$ for a tester synthetic composed of n lines with inbreeding coefficient F_x. For the BC_1- and BC_2-lines, f can be derived from their pedigrees using the path coefficient method (Falconer and Mackay, 1996). This is described in the Appendix (Section 7.3).

When inbred lines *per se* are employed as test units, the genetic variance among them can be expressed as

$$\sigma^2_t = (1+F_{t-1})\,\sigma^2_A + \frac{(1+F_{t-1})}{(1-F_{t-1})}(1-F_t)^2\,\sigma^2_D \qquad \text{(Cockerham, 1963),}$$

where F_t and F_{t-1} are the inbreeding coefficients of the inbred lines resp. of the parents of the inbred lines. For this derivation, two alleles with equal frequencies of the favourable and unfavourable allele ($p = q = 0.5$) have to be assumed.

The covariance between the genotypic effects of the test and the target units, ω_{ty}, as well as the covariance between the genotypic effects of test units used at different selection stages, $\omega_{tt'}$, are analogously derived from the pertinent covariances between relatives. The $\omega_{tt'}$ values enter into the formulae for the correlation between the selection criteria at successive selection stages, which are needed in calculating the gain from multi-stage selection. The expectations of σ^2_t, ω_{ty}, and $\omega_{tt'}$ for the various test units are summarized in Table 2.2.

Table 2.2. Genetic variances of test units and covariances between test and target units for a single trait (σ^2_t = genetic variance of test units; ω_{ty} = genetic covariance between test and target units; $\omega_{tt'}$ = genetic covariance between test units at different selection stages; TU, TU' = test units at the 1st resp. 2nd selection stage; σ^2_A, σ^2_D = additive resp. dominance variance in the S_0 base population; $\varnothing_T$ = coefficient of coancestry between two random individuals of the tester; for other abbreviations see Fig. 2.1)

TU	TU'	σ^2_t of TU	ω_{ty}	$\omega_{tt'}$
S_1L	S_2L	$1.0\,\sigma^2_A + 0.250\,\sigma^2_D$	$1.0\,\sigma^2_A$	$\sigma^2_A + 0.125\,\sigma^2_D$
S_2L	-	$1.5\,\sigma^2_A + 0.188\,\sigma^2_D$	$1.5\,\sigma^2_A$	-
DHL	-	$2.0\,\sigma^2_A$	$2.0\,\sigma^2_A$	-
$BC_1L \bullet T$	$BC_2L \bullet T$	$0.289\,\sigma^2_A + 0.578\,\varnothing_T\,\sigma^2_D$ [1]	$0.289\,\sigma^2_A$	$0.289\,\sigma^2_A$
$BC_2L \bullet T$	-	$0.385\,\sigma^2_A + 0.770\,\varnothing_T\,\sigma^2_D$ [1]	$0.385\,\sigma^2_A$	-
BC_1L_{DH} [2] $\bullet T$	BC_2L_{DH} [2] $\bullet T$	$0.313\,\sigma^2_A + 0.625\,\varnothing_T\,\sigma^2_D$ [1]	$0.313\,\sigma^2_A$	$0.313\,\sigma^2_A$
BC_2L_{DH} [2] $\bullet T$	-	$0.406\,\sigma^2_A + 0.813\,\varnothing_T\,\sigma^2_D$ [1]	$0.406\,\sigma^2_A$	-
$T \bullet S_2L$	$T \bullet S_4L$	$0.375\,\sigma^2_A + 0.750\,\varnothing_T\,\sigma^2_D$ [1]	$0.375\,\sigma^2_A$	$0.375\,\sigma^2_A$
$T \bullet S_4L$	-	$0.469\,\sigma^2_A + 0.938\,\varnothing_T\,\sigma^2_D$ [1]	$0.469\,\sigma^2_A$	-

[1] Dominance contribution has to be divided by the number of testers employed. The standard type of tester assumed is a synthetic composed of two restorer S_3-lines so that $\varnothing_T = 0.46875$.

[2] DHL are employed to produce the BC_1- resp. BC_2-lines instead of lines in segregating generations.

In calculating the phenotypic variance, σ^2_x, of the test units, the genotype x environment-interaction components of variance are assumed to be proportional to the genetic variance, irrespective of the type of test unit. The error variance is assumed to depend only on the trait and on the plot type used for evaluation but not on the genetic variance among the test units.

Estimates of the relevant variance components for the traits under selection were obtained from field trials conducted by German hybrid rye breeders during 1995-1998 and from official trials carried out by the 'Bundessortenamt' during 1992-1997. For this purpose the computer program PLABSTAT (Utz, 1996) was employed. Estimates of the ratio of additive to dominance variance and of the genetic correlation between line and testcross performance were taken from the literature (Klinger, 1985; Köhler, 1986; Wilde, 1987; Gey *et al.*, 1996; Hartmann, 1997). The estimates obtained from the various sources were averaged and 'rounded' average values were used as the standard parameter set of quantitative-genetic parameters (Table 2.3).

Table 2.3. Standard set of quantitative-genetic parameters used in the model calculations (GY = grain yield; PH = plant height; LR = lodging resistance; TKW = thousand-kernel weight; FN = falling number; LRR = leaf rust resistance; SR = single row plots; DP = drilled plots; LP, TP = line and testcross performance, resp.)

Parameter	GY [g m^{-2}]	PH [cm]	LR [score] [1]	TKW [g]	FN [s]	LRR [score] [1]
Additive variance	240	46	1.50	7.0	900	0.9
Dominance variance	120	4	0.15	1.0	100	0.1
Error variance (SR)	-	20	1.50	2.4	400	1.2
Error variance (DP)	120	10	0.70	1.2	200	0.8
Genot. x location var. [2]	0.15	0.10	0.30	0.10	0.10	0.15
Genot. x year var. [2]	0.15	0.10	0.15	0.10	0.10	0.10
Genot. x loc. x yr. var. [2]	1.00	0.30	0.90	0.40	0.40	0.60
Genet. correl. LP-TP	0.40	0.80	0.90	0.70	0.80	0.80

[1] On a 1-9 scale. [2] Genotype x environment-interaction variance relative to the genotypic variance.

2.3.2 Economic parameters

The economic weights for the traits included in the selection indices for line performance resp. for testcross performance are based on the relative economic values, REV, and the phenotypic variation of the traits. The REV follow recommendations of German hybrid rye breeders. To obtain the economic weights a_i, the REV_i are divided by the phenotypic standard deviation of the S_0-population for trait i calculated on a single-plot basis. The results are transformed such that the sum of the a_i values is one. A negative sign is finally assigned to an economic weight if selection aims at a reduction of the respective trait. The standard sets of REV and economic weights for both selection indices are reported in Table 2.4.

Table 2.4. Standard set of relative economic values (REV) and economic weights (a) used in the model calculations for the two selection indices employed

	Index for line performance		Index for testcrosss performance	
Trait	REV	a	REV	a
Grain yield [1]	-	-	6	0.240
Plant height	1	-0.056	1	-0.042
Lodging resistance	2	-0.480	2	-0.365
Thousand-kernel weight	1	0.137	1	0.104
Falling number	1	0.012	1	0.009
Leaf rust resistance	1	-0.315	1	-0.240

[1] REV and a for grain yield relate to dt ha^{-1} = 10 g m^{-2}.

The costs of the various breeding activities required in the alternative breeding schemes were determined from data provided by German hybrid rye breeders. Rounded standard costs including overheads are given in Table 2.5. The costs assumed for DHL development refer to actual expenses for DHL production in wheat by means of anther culture. At present the costs of rye DHL are much higher but it is anticipated that after adequate research efforts DHL production in rye would become as effective as in wheat. For the use of gametocides in scheme GAM1_11, flat costs of € 20,000 per cycle are assumed to cover the license fee.

Table 2.5. Standard assumptions for the costs of individual breeding activities

Breeding activity	Unit	Costs [€]
Line development and seed multiplication		
- Production of selfed seed in the field / greenhouse	1 single plant	3 / 8.75
- Production of crosses in the field / greenhouse	1 pair of plants	4 / 17.5
- Production of doubled haploid lines (DHL)	1 fertile DH plant	22.5
- Vernalisation	1 entry	0.9
- Check on male sterility	1 entry	1.1
- Seed multiplication or crossing between isolation walls / in plastic cabins	1 plot / 1 cabin	45 / 50
- Production of testcross seed (topcross)	1 entry	35
- Seed multiplication in small plastic greenhouses	1 greenhouse	500
- Production of exper. hybrids in isolation plots	1 isolation plot	1000
Evaluation of test units		
- Single row plots	1 row	5
- Drilled 5 m^2 plots	1 plot	[1] 20

[1] If number of locations exceeds five, additional costs of € 5 per plot have been assumed

2.3.3 Restrictions and additional assumptions

In the model calculations, optimum values are determined for

- the number of test units (N),
- the number of testers (T) used to assess testcross performance,
- the number of test locations (L),
- and the number of replicates (R)

at each selection stage.

As stated above, the number of candidates to be finally selected is generally set to three.

The following restrictions are imposed on the dimensioning of the trials:

- The number of locations for assessing line performance is at most three for S_2-lines and at most five for DHL due to limited seed availability.
- The total number of large drilled plots for evaluating the first type of testcross progeny (see Table 2.1) is restricted to $N*T*R \leq 20$ due to limited availability of testcross seed.
- Evaluation of line performance is always carried out in unreplicated ($R = 1$) trials.
- At least two replicates ($R \geq 2$) are employed for testcross evaluation.

Optimization is carried out under the restriction that equal monetary resources are available for each breeding scheme. The standard available budget per year is set to € 200,000. As improved lines are needed continuously, it is assumed that the breeder starts a new breeding cycle every year. Under this assumption the budget available per year - i.e. for all staggered cycles running in parallel - equals the budget available to complete one entire run of a breeding scheme.

In order to make the model calculations reflect reality as good as possible, some additional practical aspects regarding line development are considered. In producing the S_2-lines, some negative selection among the parental S_1-single plants occurs in practice. The number of S_1-plants selfed is always larger than the number of S_2-lines evaluated, as some plants exhibit e.g. incomplete seed set and are therefore discarded. The same situation occurs, even more pronounced, with S_0-plants in scheme POP2_11. In both cases, the resulting extra costs are taken into account in the model calculations. For reasons of technical security, the number of BC_0-progenies developed from each selected S_2-line resp. DHL and the number of BC_1-lines developed per BC_0-progeny is usually larger than one in practice. In the model calculations it is assumed that five BC_0-progenies and BC_1-lines are developed from each selected S_2-line or DHL. Only two of these are used to produce the testcross progenies, however, and only the testcross progenies of one BC_1-line are evaluated in the first yield trial.

2.4 Short description of the optimization procedure

In this chapter it will briefly be described how the optimum allocation of a breeding scheme is determined in the model calculations. A more detailed description of the computer programs developed for this purpose is given in the Appendix (Section 7.4).

At the beginning of the optimization process, all input parameters required are read by the program. These include (i) the quantitative-genetic and economic parameters, (ii) the relevant restrictions, and (iii) minimum and maximum values assigned to the allocation parameters to be optimized (N, T, L, R; see above). Since it is practically impossible to evaluate all potential combinations of the n allocation parameters, the optimization criterion is only calculated for a subset of these combinations using an n-dimensional grid search approach (see below). The parameter combinations must meet the restrictions given above (see Section 2.3.3). To reduce the computation time required, only practically meaningful combinations are investigated, e.g. the number of candidates is not allowed to increase from one selection stage to the next.

Furthermore, only combinations making full use of the budget are considered since all other combinations are inferior by definition.

The grid search approach is explained in the following using a hypothetical example of two parameters P1 and P2. For the first optimization step, the range of possible values for P1 and P2 is limited by their assigned minimum and maximum values (Fig. 2.2). The resulting two-dimensional plane is covered by an orthogonal grid. The criterion used for optimization is determined at all grid points. The grid point giving the best result is the provisional optimum. For the next optimization step, a smaller plane centered around the provisional optimum is investigated using a finer search grid. This procedure is repeated a few times using an ever smaller plane and an ever finer search grid until the final optimum is found.

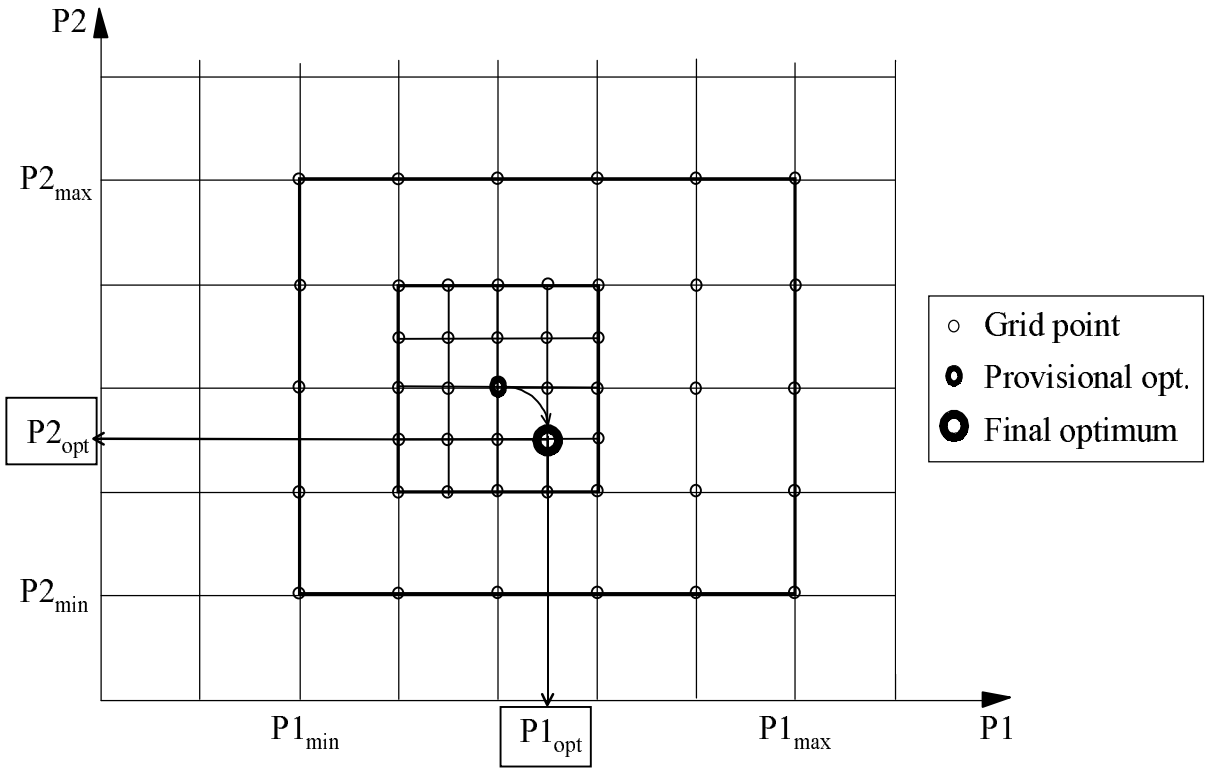

Fig. 2.2. Simple graphical representation of the grid search approach for two hypothetical parameters P1 and P2 (min, max = assigned minimum and maximum value; opt = optimum value determined in the optimization procedure)

2.5 Situations investigated

First, the optimum allocation of resources is determined for all breeding schemes employing the standard set of quantitative-genetic and economic parameters given above. Thereafter, the influence of changes in these parameters is investigated as well as the influence of deviations

from the optimum allocation of resources determined in the optimization. This procedure also allows to assess the robustness of the optimization results obtained.

One major aim of the model calculations is to find out how strongly changes in the underlying quantitative-genetic parameters affect the optimum allocation of resources and the efficiency of a breeding scheme. Therefore, the standard parameter values given in Table 2.3 are varied over a wide but genetically meaningful range.

To study the influence of the total amount of genotypic variance available in the breeding population, the additive as well as the dominance variance for all traits are halved (variant G_Low) resp. doubled (variant G_High) compared to the standard assumptions. Regarding the ratio of additive to dominance variance, two variants are investigated: (i) D_Low, in which the contribution of the dominance variance to the genotypic variance of the base population is halved for all traits, and (ii) D_High, in which the relative amount of dominance variance for all traits is doubled. The influence of changes in the error variance is investigated by halving resp. doubling the standard error variances (variants E_Low resp. E_High). Similarly, the effect of halved resp. doubled genotype x environment-interaction variances is investigated in the variants GxE_Low and GxE_High. In this respect, the question of choosing the appropriate breeding strategy to develop varieties for a given range of target environments will also be discussed.

Changes in the relative economic values assigned to the traits included in the selection indices (Table 2.4) are investigated to compare situations in which a different emphasis is put on the improvement of grain yield *versus* quality or agronomical traits. Similarly, different weights put on the improvement of line *per se* performance *versus* GCA are studied to represent less or more advanced breeding programs or breeding materials. The available budget is varied to investigate the impact of different economical situations.

In practice the dimensioning of a breeding scheme is seldom the outcome of an optimization process. Practical reasons, e.g. a limited number of test locations, may restrict the possibilities of a breeder. Therefore, the impact of deviations from the optimum allocation on the expected selection gain is also investigated.

3 Results of the model calculations

3.1 Comparison of the alternative breeding schemes under standard assumptions

The optimum allocation of the alternative breeding schemes and their expected selection gain under standard assumptions (see Section 2.3) are reported in **Table 3.1**. Since the gain in the valuation criterion is an abstract figure that doesn't give any information on the improvement of the individual component traits, the expected gain in GCA for grain yield is also given there. In the following, selection gains will always be given per year if not stated otherwise.

Table 3.1. Optimum allocation and expected yearly selection gain of the breeding schemes (N, T, L, R = no. of candidates, testers, locations, resp. replicates; G_VAL = selection gain in the valuation criterion; G_GCA_{GY} = selection gain in GCA for grain yield [$g\ m^{-2}$]; abs. = absolute magnitude; [%] = selection gain relative to that of scheme CYC1_11 under standard assumptions; LP, GCA = selection for line *per se* performance resp. for GCA)

Scheme	Selection stage	Optimum allocation				G_VAL		G_GCA_{GY}	
		N	T	L	R	abs.	[%]	abs.	[%]
CYC1_11	LP	2683	-	3					
	GCA_1	188	1	4	2	0.156	100	4.69	100
	GCA_2	21	3	11	2				
CYC1_21	LP	2816	-	3					
	GCA_11	206	1	3	2	0.147	94.2	4.45	94.9
	GCA_12	42	1	6	2				
	GCA_2	15	3	13	2				
POP2_11	LP_1	3816	-	1					
	LP_2	1091	-	3		0.135	86.5	3.90	83.2
	GCA_1	180	1	4	2				
	GCA_2	21	3	11	2				
DHL1_11	LP	937	-	3					
	GCA_1	125	1	5	2	0.168	107.7	5.06	107.9
	GCA_2	18	3	11	2				
GAM1_11	LP	2151	-	2					
	GCA_1	281	1	4	2	0.205	131.4	6.57	140.1
	GCA_2	14	3	12	2				

In the optimum allocation determined for the standard scheme CYC1_11, 2683 S_2-lines are first evaluated *per se* at three locations (Table 3.1). Evaluation is carried out in unreplicated trials as has been stated above. The best 188 candidates are selected and CMS analogues of

these genotypes are developed. The BC_1-lines of these 188 candidates are then crossed to one tester and the testcross progenies are evaluated at four locations with two replicates. The 21 best candidates are selected and their BC_2-lines are crossed to three testers. The BC_2-testcross progenies are evaluated at eleven locations with two replicates. Finally, the three most promising lines are selected for the production of experimental hybrids. With this allocation of resources, the expected gain in the valuation criterion amounts to 0.156 units per year. The expected yearly gain in GCA for grain yield is 4.69 g m^{-2}.
In the following, this variant will be called the optimum standard variant and serve as a reference. For ease of comparison, the expected gains of alternative breeding schemes and the variants studied will always be expressed in percent of the optimum standard variant if not stated otherwise.

The optimum allocation of scheme CYC1_21 clearly differs from the standard scheme with respect to testcross evaluation. A larger number of BC_1-testcrosses is first pre-evaluated at three locations. The best 20 % of these candidates are then re-evaluated in the main test at six locations. At the final selection stage, fewer BC_2-testcrosses than in the standard scheme are evaluated at a larger number of locations. The expected selection gain of CYC1_21 in the valuation criterion is 94 % of the optimum standard variant. With respect to the gain in GCA for grain yield, the relative efficiency of CYC1_21 amounts to 95 %.

Scheme POP2_11 differs from the standard scheme only with respect to selection for line *per se* performance. A large number of S_1-lines is first evaluated at only one location. Roughly the 30 % best S_2-lines are then evaluated more precisely at three locations. Testcross evaluation is identical to the standard scheme except for a slightly lower number of BC_1L-testcrosses. The selection gain of POP2_11 in the valuation criterion is only 86.5 % of the optimum standard variant. Regarding GCA for grain yield, the relative efficiency is even lower.

In scheme DHL1_11 the number of candidates at all selection stages is much lower than in the standard scheme. This difference is most pronounced for line *per se* evaluation where the optimum number of candidates for DHL1_11 is only about one third of the optimum standard variant. The evaluation intensity is practically identical to the standard scheme. Scheme DHL1_11 is 8 % superior to the standard scheme in the valuation criterion as well as in GCA for grain yield.

If gametocides are used to produce testcross progenies, the optimum allocation of resources distinctly differs from the standard scheme. With GAM1_11, fewer S_2-lines are evaluated *per se* at only two locations. A ~1.5 times higher number of candidates enter testcross evaluation. Only about five percent of them are selected so that very few testcrosses are evaluated at the last selection stage. The number of testers, locations, and replicates is again very similar to the standard scheme. With this optimum allocation of resources, the relative gain of GAM1_11 in the valuation criterion is 131 % of the optimum standard variant. The expected gain in GCA for grain yield is even 40 % higher.

The alternative breeding schemes studied differ markedly in their expected selection gain. With respect to the valuation criterion, the best scheme (GAM1_11) is 52 % superior to the least efficient scheme (POP2_11). Regarding the expected gain in GCA for grain yield this difference is even larger (68 %).

Concerning the optimum allocation of resources, the alternative schemes mainly differ in the number of candidates at the individual evaluation stages and in the number of locations to evaluate the lines *per se*. The optimum number of testers and replicates for assessing GCA proved identical for all schemes. The numbers of locations employed in the first resp. second GCA test are also very similar for all schemes studied if testcross selection is carried out as a two-stage procedure.

Marked differences between the breeding schemes exist regarding the relative costs of the individual operations belonging to the line development procedure (**Table 3.2**). In the standard scheme, 27 % of the budget are spent on producing the inbred lines and their CMS analogues as well as on the evaluation of the lines *per se*. Testcross evaluation requires ~30 % of the budget. Least money is spent on the production of testcross progenies as well as on producing experimental hybrids and multiplying the new seed-parent lines (< 8 %). For schemes CYC1_21 and POP2_11 the structure of expenditures is not much different. In contrast, more than 50 % of the budget are employed for inbred line production in scheme DHL1_11 at the expense of line *per se* evaluation and testcross production. In scheme GAM1_11 considerably less money is spent on line production since the development of CMS analogues is confined to the finally selected candidates. This postponement, however, increases the proportion of the budget spent on the production of experimental hybrids and multiplication of the new lines. Since the license fee for the gametocide (€ 20,000 per cycle) is fixed, the costs of testcross production are not increased compared to the standard scheme.

Table 3.2. Proportion of the budget spent on the individual operations belonging to the breeding procedure (TCP = testcross progenies; EH = experimental hybrids)

Breeding operation	Breeding scheme				
	CYC1_11	CYC1_21	POP2_11	DHL1_11	GAM1_11[1]
Inbred line product.[2]	26.7	25.8	30.3	56.8	18.0
Line *per se* evaluation	27.2	28.9	24.5	7.0	10.8
TCP production	7.8	8.2	7.5	3.2	7.5
TCP evaluation	30.8	31.1	30.2	26.0	34.0
EH prod.& line multipl.[3]	7.5	6.0	7.5	6.8	19.8

[1] Ten percent of the budget are spent on the gametocide. [2] Including production of CMS analogues. [3] Multiplication of finally selected seed-parent lines.

3.2 Influence of shortening the cycle length of a breeding scheme

Since breeders usually aim at a high selection gain in a short period of time, breeding scheme variants with a shortened cycle length are of particular interest. However, shortening the length of a scheme requires either a higher technological input (e.g. by using a greenhouse to produce off-season generations) and / or a lot of 'unnecessary' labour to further advance all the candidates before a selection decision regarding them is reached (see Fig. 2.1 in Section 2.1). Two schemes are investigated here to illustrate the influence of shortening the cycle length by such means.

In the first variant, the cycle length of the standard scheme CYC1_11 is reduced to ten years by developing the BC_0 and BC_1L of all selected S_2L in one year in the greenhouse (Fig. 7.5 in Appendix). Since this increases the expenses per candidate, the number of candidates at all evaluation stages and hence the overall selection intensity is reduced (**Table 3.3**). Still, the relative efficiency of this variant in the valuation criterion is 107 % of the optimum standard variant.

The second example is a variant of scheme CYC1_21 in which the BC_2-lines of all candidates are already developed in parallel to pre-testing the BC_1L-testcrosses (Fig. 7.6 in Appendix). The cycle length is thus reduced to eleven years. The optimum number of candidates in this case is affected less than in the foregoing example (Table 3.3). The number of locations for evaluating the testcross progenies is reduced. The expected selection gain in the valuation criterion surpasses that of the optimum standard variant of scheme CYC1_11 by 3 %.

Compared to the standard variant of scheme CYC1_21 with a cycle length of twelve years, the expected selection gain thus increases by 9 %.

So far, all comparisons have been made on the basis of the expected selection gain per year. However, comparing the foregoing variants with respect to their expected gain per cycle, the longest variant shows the highest relative efficiency (102 %; Table 3.3) while the shortest variant is least efficient (97 %) due to its high expenses per candidate.

Table 3.3. Influence of shortening the cycle length on the optimum allocation and expected selection gain of the breeding schemes CYC1_11 and CYC1_21 (G_CYC = selection gain in the valuation criterion expressed on a per-cycle basis; for further abbreviations see Tab. 3.1)

Scheme Cycle length	Selection stage	Optimum allocation				G_VAL		G_CYC	
		N	T	L	R	abs.	[%]	abs.	[%]
CYC1_11	LP	2683	-	3					
11 yrs.	GCA_1	188	1	4	2	0.156	100	1.72	100
	GCA_2	21	3	11	2				
CYC1_11	LP	2464	-	3					
10 yrs.	GCA_1	108	1	5	2	0.167	107.1	1.67	97.1
	GCA_2	18	3	11	2				
CYC1_21	LP	2816	-	3					
12 yrs.	GCA_11	206	1	3	2	0.147	94.2	1.76	102.3
	GCA_12	42	1	6	2				
	GCA_2	15	3	13	2				
CYC1_21	LP	2816	-	3					
11 yrs.	GCA_11	189	1	3	2	0.16	102.6	1.75	101.7
	GCA_12	37	1	5	2				
	GCA_2	18	3	11	2				

3.3 Influence of changes in the underlying parameters

In this section, the influence of changes in the quantitative-genetic and economic parameters on the optimum allocation and expected selection gain of a breeding scheme will be described for the standard scheme CYC1_11. The other schemes studied will only be discussed if they behave differently. Their relative selection gains under the various assumptions investigated are summarized in Table 7.1 in the Appendix (Section 7.5).

The optimum number of replicates for testcross evaluation was found to be identical (R = 2) for all the variants investigated. Therefore, it is not shown in the following tables any more.

3.3.1 Influence of changes in the quantitative-genetic parameters

First, the influence of the amount of **genotypic variance** in the base population will be investigated. Assuming only half the genotypic variance for all traits under selection (variant G_Low), the optimum number of locations for assessing testcross performance increases (**Table 3.4**). The number of candidates accordingly decreases at all selection stages. The expected selection gain is reduced by 30 %. Assuming doubled genotypic variances (variant G_High), more S_2-lines are evaluated *per se* at only two locations. The optimum allocation of testcross evaluation is practically unchanged. The expected gain from selection increases to 142 % of the optimum standard variant.

Table 3.4. Influence of the amount of genotypic variance in the base population on the optimum allocation and selection gain of scheme CYC1_11 (G_Low, G_High: genotypic variance of all traits halved resp. doubled compared to the standard assumptions (Table 2.3); for further abbreviations see Table 3.1)

Genotypic variance	Selection stage	Optimum allocation			G_VAL		G_GCA_{GY}	
		N	T	L	abs.	[%]	abs.	[%]
Standard	LP	2683	-	3				
	GCA_1	188	1	4	0.156	100	4.69	100
	GCA_2	21	3	11				
G_Low	LP	2513	-	3				
	GCA_1	171	1	5	0.11	70.5	3.25	69.3
	GCA_2	20	3	13				
G_High	LP	3347	-	2				
	GCA_1	189	1	4	0.222	142.3	6.70	142.9
	GCA_2	21	3	11				

Assuming a lower **relative size of dominance variance** for all traits (variant D_Low), only two testers are employed at the second stage of testcross evaluation (**Table 3.5**). The number of locations at that stage increases accordingly while the number of candidates is slightly reduced. At the other selection stages, more candidates are evaluated while the number of locations is unchanged. The selection gain in the valuation criterion increases by 12 %. If, on the other hand, a very large contribution of the dominance variance is assumed (variant D_High), the optimum number of testers increases at both stages of testcross evaluation. The number of locations as well as the number of candidates at these stages decrease accordingly. The expected selection gain is diminished by 23 %.

The expected selection gain in GCA for grain yield is much stronger affected by the relative size of dominance variance than the gain in the valuation criterion (Table 3.5). For grain yield the relative gain of the variants D_Low and D_High is 122 % resp. 51 % of the optimum standard variant.

Table 3.5. Influence of the relative size of dominance variance on the optimum allocation and selection gain of scheme CYC1_11 (D_Low, D_High: contribution of the dominance variance to the genotypic variance of the S_0-population halved resp. doubled compared to the standard assumptions (Table 2.3); for further abbreviations see Table 3.1)

Dominance variance	Selection stage	Optimum allocation			G_VAL		G_GCA_{GY}	
		N	T	L	abs.	[%]	abs.	[%]
Standard	LP	2683	-	3				
	GCA_1	188	1	4	0.156	100	4.69	100
	GCA_2	21	3	11				
D_Low	LP	2798	-	3				
	GCA_1	198	1	4	0.175	112.2	5.74	122.4
	GCA_2	20	2	14				
D_High	LP	2689	-	3				
	GCA_1	144	2	3	0.12	76.9	2.41	51.4
	GCA_2	19	5	9				

The influence of the relative size of dominance variance is basically similar for all breeding schemes studied. Assuming high dominance variances, the optimum number of testers at the first testcrossing stage is two for all schemes studied. In scheme CYC1_21, the number of locations to evaluate the BC_1L-testcrosses is accordingly reduced to two in the pre-test and three in the main test since there is only enough testcross seed for a limited number of large drilled plots (see Section 2.3.3). The optimum number of testers at the second testcrossing stage is increased to even six for schemes CYC1_21, DHL1_11 and GAM1_11.

The superiority of scheme GAM1_11 over the standard scheme decreases with increasing dominance variances from 33 % in variant D_Low to 28 % in variant D_High (Table 7.1 in Appendix). The relative efficiency of scheme CYC1_21 is also slightly lower for higher dominance variances.

The influence of the **error variance** on the optimum allocation and the expected selection gain of scheme CYC1_11 is shown in **Table 3.6**. Assuming halved error variances (variant E_Low) for all traits and both plot types, i.e. single row plots and large drilled plots, only the

optimum number of locations for evaluating the lines *per se* is reduced. The number of locations at the other selection stages as well as the numbers of testers and replicates remain unchanged. In this context it is emphasized that the number of replicates for assessing testcross performance is assumed to be at least two (see Section 2.3.3). The number of S_2-lines evaluated clearly increases whereas the number of BC_1L- and BC_2L-testcrosses is almost unaffected. The expected selection gain is practically unchanged. Assuming doubled error variances (variant E_High), the number of locations for assessing testcross performance increases and fewer candidates are evaluated at all stages. The expected selection gain in the valuation criterion is again hardly affected whereas the gain in GCA for grain yield is reduced by 2 %.

Table 3.6. Influence of the size of the error variance on the optimum allocation and selection gain of scheme CYC1_11 (E_Low, E_High: error variances halved resp. doubled for all traits and both plot types compared to the standard assumptions; for abbreviations see Table 3.1)

Error variance	Selection stage	Optimum allocation			G_VAL		G_GCA_{GY}	
		N	T	L	abs.	[%]	abs.	[%]
Standard	LP	2683	-	3				
	GCA_1	188	1	4	0.156	100	4.69	100
	GCA_2	21	3	11				
E_Low	LP	3347	-	2				
	GCA_1	189	1	4	0.157	100.6	4.74	101.1
	GCA_2	21	3	11				
E_High	LP	2513	-	3				
	GCA_1	171	1	5	0.155	99.4	4.60	98.1
	GCA_2	20	3	13				

The relative superiority of schemes DHL1_11 and GAM1_11 over the standard scheme is slightly lower for smaller error variances (Table 7.1 in Appendix). The relative efficiency of the other schemes is not affected by changes in this parameter.

To demonstrate the influence of the **genotype x environment -interaction** (G x E) variance, optimization results assuming different magnitudes of the respective interactions are given in **Table 3.7**. As can be seen immediately, the influence of the G x E variance on the expected selection gain is much more pronounced than that of the error variance. Assuming halved G x E variances (variant GxE_Low), fewer locations are necessary at all evaluation stages. Correspondingly, more candidates are evaluated at all stages. The expected gain from

selection in the valuation criterion increases by 6 %. Assuming higher G x E variances (variant GxE_High), the opposite effect is observed: the optimum number of locations increases while the number of candidates is reduced. The expected selection gain under these assumptions decreases by 8 %.

The difference between variants GxE_Low and GxE_High is again more pronounced for the expected selection gain in GCA for grain yield than for the gain in the valuation criterion. For grain yield the relative selection gains of variants GxE_Low and GxE_High are 107 % resp. 90 % of the gain under standard assumptions.

The relative efficiency of schemes CYC1_21 and DHL1_11 increases with larger amounts of G x E variance (Table 7.1. in Appendix), while that of the other schemes is hardly affected.

Table 3.7. Influence of the size of the genotype x environment-interaction variance on the optimum allocation and selection gain of CYC1_11 (GxE_Low, GxE_High: components of genotype x environment-interaction variance halved resp. doubled compared to the standard assumptions; for further abbreviations see Table 3.1)

G x E variance	Selection stage	Optimum allocation			G_VAL		G_GCA$_{GY}$	
		N	T	L	abs.	[%]	abs.	[%]
Standard	LP	2683	-	3				
	GCA_1	188	1	4	0.156	100	4.69	100
	GCA_2	21	3	11				
GxE_Low	LP	3449	-	2				
	GCA_1	207	1	3	0.166	106.4	5.02	107
	GCA_2	24	3	9				
GxE_High	LP	2513	-	3				
	GCA_1	171	1	5	0.143	91.7	4.23	90.2
	GCA_2	20	3	13				

The large impact of the G x E variances on the expected selection gain has consequences with respect to an important question in practical breeding: the choice of the appropriate breeding strategy to develop varieties for a given range of target environments. Usually, the target area consists of a broad range of environments that differ with respect to climatic and edaphic factors, cultivation practices etc. The breeder thus has to decide between two basic strategies: (i) to develop varieties specifically adapted to particular environmental or growing conditions in separate smaller breeding programs or (ii) to employ a single breeding program aiming at

genotypes adapted to the whole range of environments. Which of these strategies is more promising, essentially depends on the importance of the G x E variances. It is assumed here that these variances increase with increasing environmental heterogeneity of the target area.

The optimum allocation and expected gain of scheme CYC1_11 considering a target area that consists of two different agro-ecological zones and the two strategies described above are given below. The first strategy ('Specific') employs the optimum standard variant of scheme CYC1_11 in each of the two zones. For the second strategy ('Broad'), two situations are compared in which the G x E variances are increased to a different extent (variants A and B). The budget of the one large breeding program is twice that of the two zone-specific standard programs so that in total the same budget is available for both strategies.

With strategy 'Broad', the number of candidates entering the breeding program is about twice that of a zone-specific program resulting in a higher overall selection intensity (**Table 3.8**). The number of locations for assessing testcross performance is also higher. Employing one single program across the two zones is preferable as long as the relative increase of the G x E variances is not too strong. Assuming e.g. an 1.5-fold increase of the interaction variances, strategy 'Broad' results in a 5 % higher selection gain than strategy 'Specific'. If the relative size of the interaction variances is augmented further, however, the gain of one large breeding program is reduced and two zone-specific breeding programs are to be preferred.

Table 3.8. Optimum allocation and selection gain of CYC1_11 assuming different breeding strategies for two environmentally divergent target zones (Specific = two separate breeding programs; Broad = one large breeding program; Variant A, B = G x E variances multiplied by 1.5 resp. 2.5 compared to the standard assumptions; for further abbreviations see Table 3.1)

Strategy	Selection stage	Optimum allocation			G_VAL		G_GCA$_{GY}$	
		N	T	L	abs.	[%]	abs.	[%]
Specific	LP	2683	-	3				
	GCA_1	188	1	4	0.156	100	4.69	100
	GCA_2	21	3	11				
Broad	LP	5707	-	3				
Variant A	GCA_1	333	1	5	0.163	104.5	4.93	105.1
	GCA_2	30	3	16				
Broad	LP	5256	-	3				
Variant B	GCA_1	315	1	6	0.151	96.8	4.53	96.6
	GCA_2	28	3	18				

3.3.2 Influence of changes in the economic parameters

The expected selection gain does not only depend on the quantitative-genetic parameters but also on economic factors like the available budget. Additionally, the relative efficiency of breeding schemes may differ depending on the main goal of the breeding program. For example, one breeding program may mainly aim to improve grain yield while another puts more emphasis on disease resistance or quality. Similarly, different weights may be given to the improvement of line performance resp. GCA.

To compare breeding programs putting a different emphasis on grain yield *versus* the remainder traits, the **relative economic value (REV) assigned to grain yield** in the selection index for testcross performance has been varied. Assuming half the standard REV for grain yield, the optimum number of candidates increases at all selection stages (**Table 3.9**). Only two testers instead of three are used to produce the BC_2L-testcrosses. The expected gain in GCA for grain yield is reduced to 72 % of the optimum standard variant whereas the gain in GCA for plant height increases to 148 %. The gain in the other quality and agronomical traits is augmented correspondingly (data not shown). Putting an even stronger emphasis on grain yield than in the standard variant by doubling its REV causes only a slight change in the number of candidates. The gain in GCA for grain yield is increased by 13 % whereas the gain in GCA for plant height and the other traits is markedly reduced by about 45 %.

Table 3.9. Influence of the relative economic value assigned to grain yield (REV_{GY}) on the optimum allocation and expected selection gain of scheme CYC1_11 (for REV of the other traits see Table 2.4; G_GCA_{PH} = selection gain in GCA for plant height [cm]; for further abbreviations see Table 3.1)

REV_{GY}	Selection stage	Optimum allocation			G_GCA_{GY}		G_GCA_{PH}[1]	
		N	T	L	abs.	[%]	abs.	[%]
6	LP	2683	-	3				
(= Standard)	GCA_1	188	1	4	4.69	100	-0.194	100
	GCA_2	21	3	11				
3	LP	2863	-	3				
	GCA_1	198	1	4	3.38	72	-0.287	148.4
	GCA_2	22	2	12				
12	LP	2740	-	3				
	GCA_1	180	1	4	5.28	112.6	-0.108	55.9
	GCA_2	22	3	11				

[1] Selection gain in plant height is negative as selection aims at a reduction of this trait.

The relative efficiency of scheme POP2_11 is higher if less emphasis is put on grain yield (Table 7.1 in Appendix). In contrast, the superiority of scheme GAM1_11 over the standard scheme increases from 29.5 % assuming a low REV for grain yield to 33 % assuming a high value.

Breeding programs may also differ regarding the **emphasis put on the improvement of line performance *versus* GCA**. Giving a larger weight to line *per se* performance is necessary in the beginning of hybrid breeding or if the breeding materials used have not yet undergone intense selection at the inbred level. The more advanced the breeding program or the breeding materials, the more weight will be put on the improvement of GCA. If a larger weight is assigned to line performance, the optimum number of S_2-lines evaluated *per se* is drastically increased while the number of testcross progenies evaluated is severely reduced (**Table 3.10**). The numbers of testers and locations remain almost unchanged. The expected selection gain in the total economic value regarding line performance increases to 125% of the optimum standard variant whereas the respective gain in GCA decreases to 91 %. Assuming, on the other hand, a very high weight on GCA, only half as many S_2-lines as in the standard variant are evaluated *per se* at only two locations. The number of candidates entering testcross evaluation is markedly increased. Evaluation intensity in this phase is not changed. The expected gain in line performance is reduced to 68 % of the optimum standard variant whereas the gain in GCA increases to 105 %.

Table 3.10. Influence of the weights given to the gain in line performance resp. GCA (W_{LP} resp.W_{GCA}) in calculating the optimization criterion on the optimum allocation and selection gain of scheme CYC1_11 (G_LP, G_GCA = yearly selection gain in the total economic value regarding line performance resp. regarding GCA; for further abbreviations see Table 3.1)

W_{LP} : W_{GCA}	Selection stage	Optimum allocation			G_LP		G_GCA	
		N	T	L	abs.	[%]	abs.	[%]
0.25 : 0.75	LP	2683	-	3				
(= Standard)	GCA_1	188	1	4	0.154	100	0.157	100
	GCA_2	21	3	11				
0.40 : 0.60	LP	4501	-	3				
	GCA_1	99	1	5	0.193	125.3	0.143	91.1
	GCA_2	17	3	11				
0.10 : 0.90	LP	1358	-	2				
	GCA_1	266	1	4	0.105	68.2	0.165	105.1
	GCA_2	23	3	11				

Schemes CYC1_21 and GAM1_11 show a higher relative efficiency if more weight is put on GCA improvement. For CYC1_21 the expected gain in the valuation criterion relative to that of the standard scheme increases from 92.6 % for $W_{GCA} = 0.6$ to 95 % for $W_{GCA} = 0.9$ (Table 7.1 in Appendix). An even stronger increase in relative efficiency is observed for GAM1_11. In contrast, the relative gain of POP2_11 decreases with increasing weight on GCA.

Breeding programs may strongly differ with respect to the **available budget**. Therefore, it is important to study (i) the effect of the budget on the optimum allocation and (ii) whether changes of the budget affect alternative breeding schemes to a different extent and maybe even lead to changes in the ranking.

The influence of the available budget on the optimum allocation of scheme CYC1_11 is shown in **Table 3.11**. Obviously, differences in the budget mainly affect the number of candidates evaluated. Assuming half the standard budget, i.e. € 100,000 per year, the number of candidates at the first two stages of selection is halved compared to the optimum standard variant. At the last selection stage, the number of candidates is also decreased by one third and the number of testers and locations is reduced as well. The selection gain in the valuation criterion decreases by 10 %. The gain in GCA for grain yield is even stronger diminished. With an available budget of € 400,000 per year, the number of candidates at all three selection stages is markedly increased and the testcrosses are evaluated at more locations. The number of testers to produce the BC_2L-testcrosses is also larger. The selection gain in the valuation criterion increases by 9 %, the gain in GCA for grain yield by 11 %.

Table 3.11. Influence of the available budget on the optimum allocation and selection gain of scheme CYC1_11 (for abbreviations see Table 3.1)

Budget [€]	Selection stage	Optimum allocation			G_VAL		G_GCA_{GY}	
		N	T	L	abs.	[%]	abs.	[%]
100,000	LP	1256	-	3				
	GCA_1	99	1	4	0.141	90.4	4.09	87.2
	GCA_2	15	2	9				
200,000	LP	2683	-	3				
(= Standard)	GCA_1	188	1	4	0.156	100	4.69	100
	GCA_2	21	3	11				
400,000	LP	5703	-	3				
	GCA_1	342	1	5	0.170	109.0	5.22	111.3
	GCA_2	29	4	12				

Figure 3.1 illustrates the relative selection gain as a function of the available budget for the five breeding schemes studied. Over the range of budgets investigated (€ 100,000 to € 400,000) no change of ranking occurs. The curves are flattening with increasing budget illustrating the diminishing returns on investment. Roughly said, doubling the budget leads to a ten percent increase in the expected selection gain over the range of budgets studied. Interestingly, substituting scheme GAM1_11 for scheme CYC1_11 would lead to a greater increase in the selection gain than doubling the available budget for the latter.

The relative superiority of schemes DHL1_11 and GAM1_11 increases with higher budgets. Compared to the respective optimum variant of the standard scheme, the relative superiority of scheme DHL1_11 is 6 % resp. 8 % for a budget of € 100,000 resp. € 400,000 (Table 7.1 in Appendix). An even stronger influence is observed for scheme GAM1_11, for which the relative superiority over CYC1_11 increases from 27 % assuming a budget of € 100,000 to 33 % with a budget of € 400,000. The relative superiority of the best scheme (GAM1_11) over the worst scheme (POP2_11) increases from 47 % to 54 % over the range of budgets investigated.

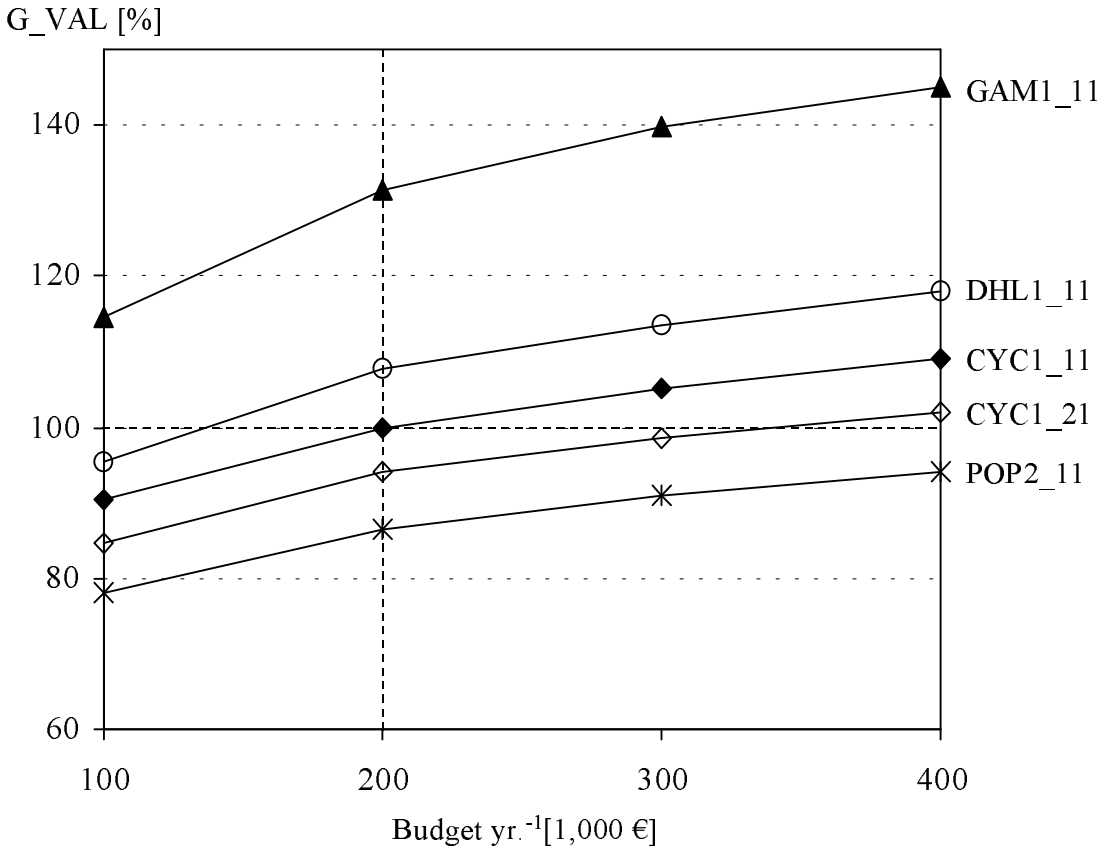

Fig. 3.1. Relative selection gain of the breeding schemes investigated as a function of the available budget per year (G_VAL [%]: selection gain in the valuation criterion relative to that of the standard scheme CYC1_11 under standard assumptions)

3.4 Influence of deviations from the optimum allocation

According to the optimization results, the optimum **numbers of testers** at the first and second stage of testcrossing are low under standard assumptions and moderate to high if high dominance variances are assumed (see Section 3.3.1). The consequences of deviations from the optimum numbers of testers determined in the model calculations are reported in the following.

Under standard assumptions, the expected selection gain of scheme CYC1_11 in the valuation criterion is hardly affected if the numbers of testers do not deviate too much from the optimum (**Fig. 3.2**; **Table 3.12**). A relative efficiency below 99 % results only if (i) one tester is used at both stages of testcrossing or (ii) three testers are used at the first testcrossing stage. With increasing numbers of testers, the number of candidates and locations at all evaluation stages decreases (Table 3.12). The gain in GCA for grain yield is stronger affected by deviations from the optimum number of testers than the gain in the valuation criterion (Table 3.12). For this trait, the optimum number of testers at the second testcrossing stage is slightly higher than for the index trait (data not shown).

Table 3.12. Optimum allocation and selection gain of scheme CYC1_11 assuming different numbers of testers at the first and second stage of testcrossing (T_1 and T_2, resp.; for further abbreviations see Table 3.1)

No. of testers	Selection stage	Optimum allocation[1]			G_VAL		G_GCA_{GY}	
		N	T	L	abs.	[%]	abs.	[%]
$T_1 = 1$	LP	3070	-	3				
$T_2 = 1$	GCA_1	207	1	4	0.153	98.1	4.41	94
	GCA_2	23	1	15				
$T_1 = 2$	LP	2643	-	3				
$T_2 = 4$	GCA_1	153	2	3	0.155	99.4	4.65	99.1
	GCA_2	18	4	11				
$T_1 = 3$	LP	2472	-	3				
$T_2 = 6$	GCA_1	135	3	3	0.154	98.7	4.58	97.7
	GCA_2	16	6	8				

[1] Optimum number of replicates for GCA evaluation is identical (R = 2) for all variants.

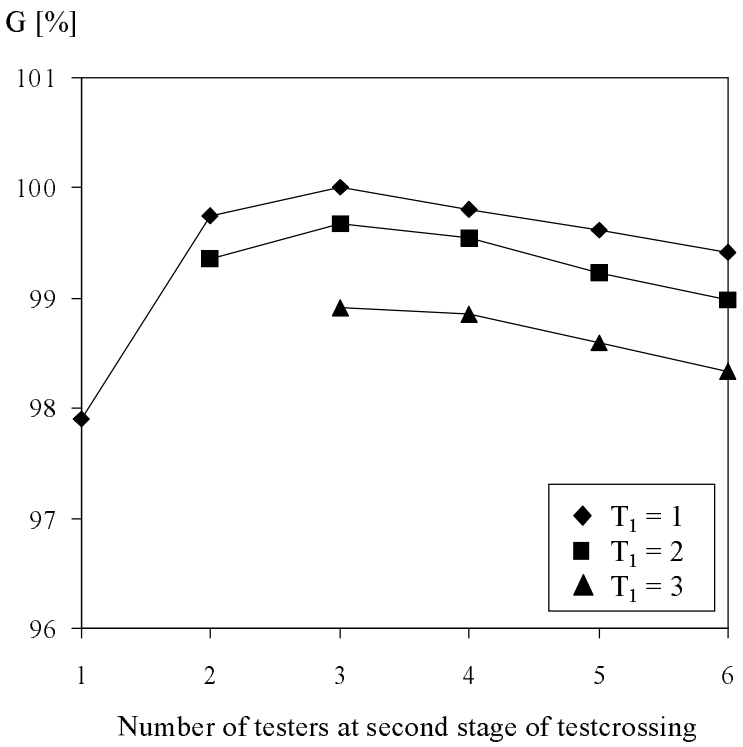

Fig. 3.2. Relative selection gain (G [%]) of scheme CYC1_11 as a function of the number of testers at the second stage of testcrossing (T_2) assuming one to three testers at the first stage of testcrossing (T_1) and standard dominance variances (Restriction: $T_2 \geq T_1$)

Assuming low dominance variances (Variant D_Low, see Section 3.3.1), using more testers than optimum leads to a stronger reduction of the expected selection gain than under standard assumptions, especially if two or three testers are used at the first testcrossing stage (**Fig. 3.3**). In the range of two to six testers at the second testcrossing stage, the decrease is almost linear. The opposite is observed if high dominance variances are assumed (Variant D_High). In this case, the expected selection gain is markedly reduced if few testers are used at both testcrossing stages, especially if only one tester is used at the first stage (**Fig. 3.4**). With two or three testers at the first and four to six testers at the second stage of testcrossing, the expected selection gain is always maximized.

Assuming low or high dominance variances, the gain in GCA for grain yield is again stronger affected by deviations from the optimum number of testers than the gain in the valuation criterion (data not shown). With high dominance variances, the optimum number of testers at the second stage to assess GCA for grain yield is again slightly higher than for the index trait. The optimum numbers of candidates and locations for a given number of testers do not differ much from those reported in Table 3.12 (data not shown).

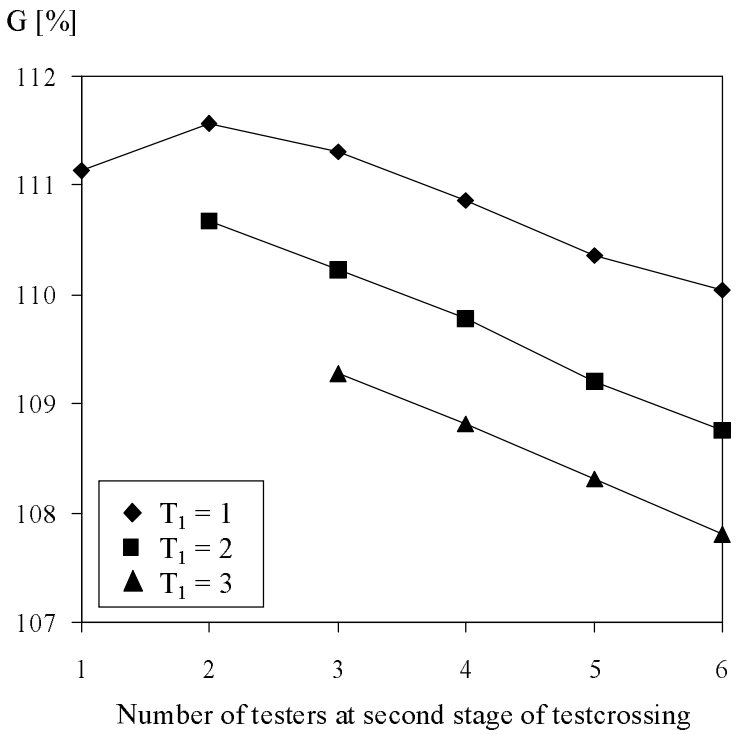

Fig. 3.3. Relative selection gain (G [%]) of scheme CYC1_11 as a function of the number of testers at the second stage of testcrossing (T_2) assuming one to three testers at the first stage of testcrossing (T_1) and low dominance variances (Variant D_Low, see Section 3.3.1; Restriction: $T_2 \geq T_1$)

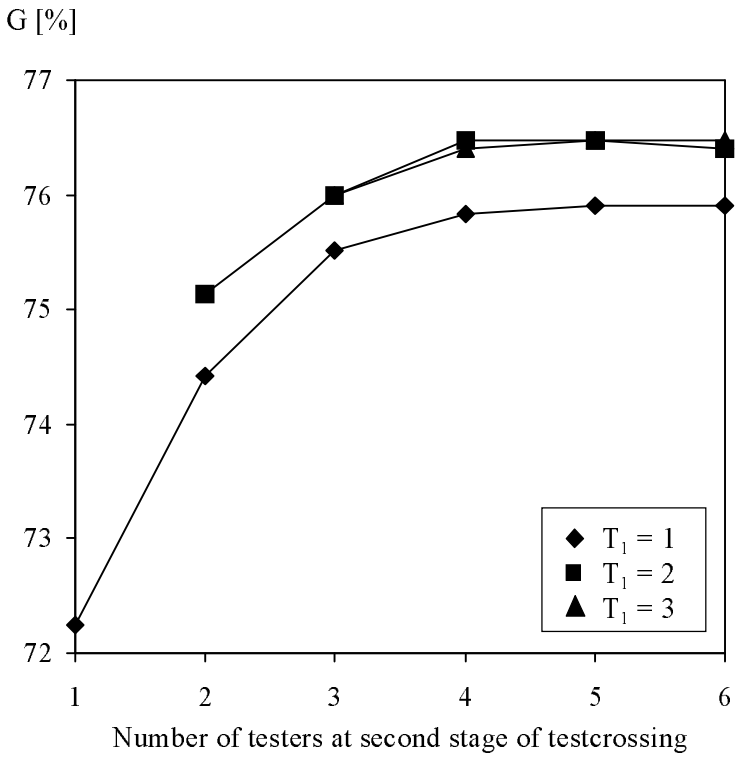

Fig. 3.4. Relative selection gain (G [%]) of scheme CYC1_11 as a function of the number of testers at the second stage of testcrossing (T_2) assuming one to three testers at the first stage of testcrossing (T_1) and high dominance variances (Variant D_High, see Section 3.3.1; Restriction: $T_2 \geq T_1$)

The influence of the number of testers is similar for all breeding schemes studied. Assuming standard or low dominance variances, using more testers than optimum - especially at the first testcrossing stage - leads to a slightly stronger reduction of the expected selection gain of schemes GAM1_11 and CYC1_21 compared to the standard scheme.

Another important aspect is the number of **locations** available in a breeding program. For various reasons this number might be much lower than the optimum number determined in the model calculations, particularly at the final evaluation stage. In the range of the optimum eleven to four locations available, the selection gain of scheme CYC1_11 in the valuation criterion decreases by only 2 % (**Fig. 3.5**). From four to one locations, the expected selection gain is much stronger diminished by additional 13 %. Regarding the gain in GCA for grain yield, a stronger decrease is already observed for less than five locations. Over the whole range investigated, the selection gain in this trait is reduced by almost 20 %.

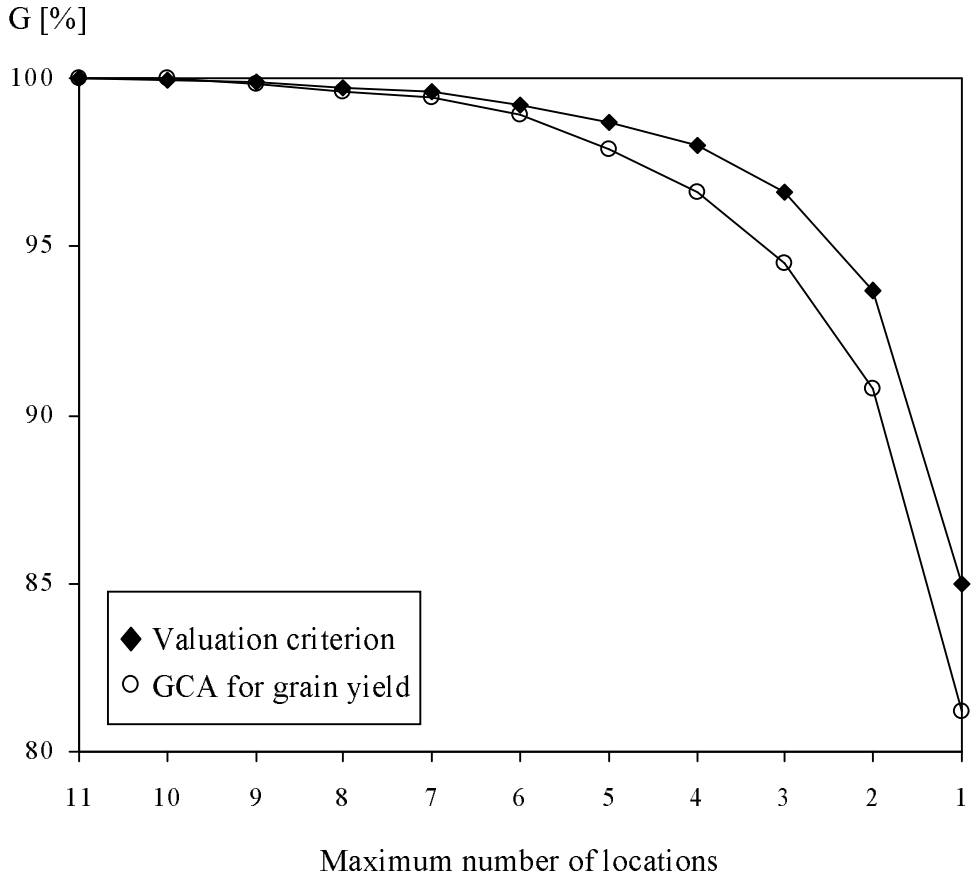

Fig. 3.5. Relative selection gain (G [%]) of scheme CYC1_11 in the valuation criterion and in GCA for grain yield as a function of the maximum number of available locations (Restriction: number of locations is not allowed to decrease from one evaluation stage to the next)

Limiting the number of available locations causes marked changes in the optimum allocation of resources. Assuming a maximum of five testers and replicates for assessing GCA, only the number of candidates at all evaluation stages increases as long as more than seven locations are available for scheme CYC1_11. Below that value, first the number of testers at the second testcrossing stage increases followed by an increase in the number of replicates at that stage (**Table 3.13**). For only one or two location(s), the number of testers and replicates at the first testcrossing stage are enhanced, too (data not shown).

Table 3.13. Optimum allocation and selection gain of scheme CYC1_11 assuming different maximum numbers of locations (Restrictions: $T \leq 5$, $R \leq 5$, no. of locations is not allowed to decrease from one selection stage to the next; for further abbreviations see Table 3.1)

Maximum no. of locations	Selection stage	Optimum allocation				G_VAL		G_GCA_{GY}	
		N	T	L	R	abs.	[%]	abs.	[%]
11	LP	2683	-	3					
	GCA_1	188	1	4	2	0.156	100	4.69	100
	GCA_2	21	3	11	2				
5	LP	3021	-	3					
	GCA_1	198	1	4	2	0.154	98.7	4.59	97.9
	GCA_2	23	4	5	2				
3	LP	3115	-	3					
	GCA_1	207	1	3	2	0.151	96.8	4.43	94.5
	GCA_2	22	4	3	4				

The relationship between the number of locations and the relative expected selection gain is very similar for all breeding schemes studied. The selection gain achievable with only one or two location(s) relative to that in the optimum is slightly lower for scheme POP2_11 than for the standard scheme and slightly higher for schemes GAM1_11 and CYC1_21.

4 Discussion

4.1 Discussion of the model

The reliability of a model study depends on the extent to which the model assumptions and parameters reflect reality. In the following, the assumptions made in the present study will be discussed in this respect.

4.1.1 Quantitative-genetic and economic parameters and assumptions

To give results that are of practical value, model calculations require reliable **estimates of the relevant quantitative-genetic parameters**. A number of studies to estimate quantitative-genetic parameters in rye have been carried out over the last decades (Mechelke, 1981; Górny *et al.*, 1982; Klinger, 1985; Köhler, 1986; Wilde, 1987; Loock, 1991; Rattunde *et al.*, 1991; Wehmann *et al.*, 1991; Ludwig, 1992; Gey *et al.*, 1996; Erfurt, 1997; Hartmann, 1997). However, as population parameters may change over the course of time, it is important to base the model calculations on present figures. Current estimates of the relevant parameters were therefore obtained from recent field trials conducted by German hybrid rye breeders and the 'Bundessortenamt' (see Section 2.3.1). The estimates mainly correspond well with figures reported in the literature (see references above).

All traits included in the selection indices are assumed to be uncorrelated. Estimates obtained from breeders' trials revealed low to intermediate positive genetic **correlations** between most of the **traits** of interest (data not shown). Intermediate positive as well as intermediate negative correlations were, however, observed between (i) grain yield and plant height and (ii) grain yield and lodging resistance, in different years. The relationship among these three traits is explained by the important role of the culm as an assimilation organ in rye. As long as no lodging occurs, the correlation between plant height and grain yield is thus usually positive whereas a negative relationship is observed if the plants are lodging. Low to intermediate correlation coefficients of sometimes opposite sign are also reported in the literature (Geiger, 1982; Klinger, 1985; Köhler, 1986; Wilde, 1987; Loock, 1991; Hartmann, 1997). Due to these opposing results, correlations have been ignored in the present model calculations.

It is assumed that the base population is in **gametic phase equilibrium**. Deviations from gametic phase equilibrium in a population can arise from the intermixture or intercrossing of genotypes from populations with different gene frequencies (Falconer and Mackay, 1996). A negative gametic phase disequilibrium (GPD) diminishes the genetic variance and thus

reduces the expected gain from selection (Bulmer, 1971). Negative GPD in the base population would be expected if the genotypes intermated carry complementary alleles regarding the traits of interest, which might be the case in second cycle breeding programs (Melchinger, 1984). An existing GPD can only be reduced by recombination in the population. This would increase the cycle length of a breeding scheme, however. The significance of recombination in second cycle breeding programs is discussed by Melchinger (1984). In an experimental study in maize he found that recombination in the seed and pollinator parent population prior to crossing increased the genetic variance of their hybrid population but decreased its mean, so that on the whole the chances of selecting lines with superior GCA were not increased.

Comparatively little is known about the importance of **epistatic and reciprocal effects** in rye (Geiger and Becker, 1984). Extensive studies in maize have shown that epistatic variances are of minor importance compared to additive and dominance variance (Hallauer and Miranda, 1981). Neglecting them in the model calculations thus seems justified.

Estimates of the additive and dominance variance have been obtained from field trial data on the performance of inter-pool crosses. Regarding testcross progeny evaluation, these are the relevant parameters because the genotypic variance of the hybrid population is of interest here. The **genetic variance among testcross progenies** can be derived from the foregoing parameters without imposing any restriction on the number or frequency of alleles involved. If, however, these estimates are used to calculate the **genetic variance among inbred lines**, two assumptions are necessary. First, one has to assume that there is no significant difference between the genetic variance components obtained from inter-pool and intra-pool crosses. Population parameter estimates of Klinger (1985) support this assumption. Moreover, equal allele frequencies ($p = q = 0.5$) have to be assumed to express the variance in any generation of inbreeding as a function of the additive and dominance variance in the base population since otherwise covariances between additive and dominance variance have to be accounted for (Cockerham, 1963). The latter assumption seems to be justified by the fact that the genetic variance of a quantitative trait is mainly determined by loci carrying alleles of intermediate frequency (Falconer and Mackay, 1996). Loci exhibiting rather extreme allele frequencies contribute only minor portions to the total genetic variance.

In calculating the **phenotypic variance** among test units, it is assumed that the components of genotype x environment-interaction (G x E) variance are proportional to the genotypic

variance of the test units. This assumption is in agreement with the general observation that the size of the G x E variance increases with increasing homozygosity and homogeneity of the test units (Becker and Léon, 1988). A proportional relationship between the genotypic variance of different hybrid types and their G x E variance was found in maize (Eberhart and Russell, 1969; Schnell and Becker, 1986; Geiger *et al.*, 1987) and in rye (Becker *et al.*, 1982). Considering the often large estimation errors of quantitative-genetic parameters, a more complicated model to calculate the G x E variances does not seem appropriate here.
In contrast to the G x E variances, the error variance is assumed to be constant for a given trait and plot type (single row or large drilled plot), irrespective of the genotypic variance of the test unit. This is in agreement with results of Sprague and Federer (1951) who observed similar error variances for different hybrid types of maize. The estimates obtained for the present study from breeders' trials and official trials also support this assumption (data not shown).

To allow a fair comparison of the alternative breeding schemes, optimization is carried out under the restriction of a **fixed available budget** per year. Alternatively, a fixed annual labour capacity could have been used. However, as the costs of a breeding program are largely overhead costs caused by e.g. personnel, land, greenhouses, and machinery (Müller and Zeddies, 1988), taking only the (variable) amount of labour into account may lead to biased results. The **costs of the individual breeding steps** underlying this study therefore include overheads. They have been derived from data provided by German hybrid rye breeders. Obviously, these costs may differ among breeding stations and are also subject to changes over time. However, as long as the ratio of the individual costs remains similar, the conclusions drawn from the model calculations will not be affected significantly. The **relative economic values** used to construct the selection indices follow recommendations of German hybrid rye breeders, too. The values were thought to represent the actual importance of the traits in practical breeding. Changes in the breeding goal may of course lead to a different set of relative economic values.

4.1.2 Additional restrictions

In the model calculations the **number of finally selected candidates** is fixed at three. This is thought to be a reasonable number from a breeder's point of view as at the last stage of selection the small differences between the best and the next best candidate(s) are very difficult to assess. Moreover, differences between the best candidates regarding single traits, e.g. quality traits or disease resistances, can be used to complement the specific strenghts and

weaknesses of different restorer synthetics employed as pollinators. The breeding schemes investigated have also been optimized under the assumptions that (i) only the very best line is selected or (ii) the five best lines are finally chosen (data not shown). The expected gain from selection increases with a decreasing number of finally selected candidates. The ranking and relative efficiency of the breeding schemes are not affected, however.

The phenotypic variance of the candidates and the correlation between selection and gain criterion depend on the number of environments employed for evaluation (see Section 2.2.1). From a theoretical point of view, it would be optimum to carry out unreplicated trials at a very large number of locations. In spite of this, the **minimum number of replicates to assess testcross performance** is fixed at two in the model calculations. This restriction was chosen for practical reasons. First, additional testing efforts are required to estimate the experimental error if trials are unreplicated, which would consequently reduce the number of candidates. Moreover, it will generally be easier and more cost-efficient to have two replicates at a moderate number of locations than to employ almost twice as many locations with only one replicate. Without this restriction, the optimum number of replicates of scheme CYC1_11 under standard assumptions reduces to one at all evaluation stages while the number of locations for assessing testcross performance increases strongly. More candidates are evaluated at all stages (additional testing efforts to estimate the experimental error - as mentioned above - were not considered in this variant). The expected gain from selection increases by 1.6 % (data not shown).

4.1.3 Selection procedure

Each breeding scheme studied is subdivided into two phases of selection that are treated separately. This corresponds well with practical hybrid rye breeding. Pre-evaluating the lines *per se* before selecting for combining ability is considered absolutely necessary by breeders (Knopf, Wilde, Wortmann; pers. comm.). It is a cheap and effective way to reduce the number of candidate lines remaining for the expensive breeding phases of (i) conversion into CMS analogues, (ii) production of testcrosses, and (iii) testcross evaluation in large drilled plots.

Selection is assumed to be based on a **selection index**. A characteristic of index selection is that weaknesses in one or a few trait(s) can be counterbalanced by strengths in other traits. This is a meaningful approach in RS, but may pose a problem in parent line developement since the selected genotypes must meet certain minimum standards for each trait of interest here. Therefore, breeders generally use independent culling levels to meet these requirements.

The calculation of the expected gain from independent culling level selection is, however, very cumbersome, even for only a few traits (Wricke and Weber, 1986). Thus, with five or six traits and as many as three stages of selection considered, the use of independent culling level selection was not manageable.

A practical consequence of the need to meet certain minimum standards for each trait is that the number of candidates entering a breeding program must certainly be larger than the optimum number obtained by the present model calculations. Consequently, the evaluation intensity would have to be reduced. This would diminish the expected selection gain, especially in the DHL-scheme, for which the optimum number of candidates initially evaluated is very small compared to the other schemes. The impact of employing a minimum number of candidates at the first selection stage on the allocation and expected selection gain of schemes CYC1_11 and DHL1_11 is shown in **Table 4.1**. For both schemes, the minimum number assumed is roughly double the optimum number obtained in the model calculations: at least 5000 S_2-lines must be evaluated with scheme CYC1_11 and at least 1750 DHL with scheme DHL1_11. Under these assumptions the number of locations at the first selection stage is reduced to two (Table 4.1). With scheme CYC1_11, about 20 % fewer testcross progenies are evaluated at both stages of testcross selection and fewer locations are used at the last selection stage. The expected selection gain in the valuation criterion is hardly diminished but the gain in GCA for grain yield decreases by 5 %. With scheme DHL1_11, the number of testcrosses is severely reduced by 40 %. Besides fewer locations, fewer testers are used at the last evaluation stage. As a consequence, the gain in the valuation criterion is reduced by 2 %. The expected gain in GCA for grain yield is strongly diminished by 13 %, so that in this respect scheme DHL1_11 even becomes inferior to scheme CYC1_11.

In calculating both the optimization and the valuation criterion only the direct selection gains in line performance resp. in GCA are considered. However, as line and testcross performance are correlated, selection on the former also leads to an indirect selection gain in the latter and *vice versa*. Yet, employing the total selection gain as optimization criterion is not possible. The reason for this is that the selection index for line performance doesn't comprise grain yield because (i) the correlation between line performance and testcross performance is too weak for this trait and (ii) assessing grain yield in single row plots would not be meaningful. An *indirect* improvement of GCA by selection for line performance is thus only possible for the other component traits. Therefore, a drastical shift in the optimum allocation of resources is observed if the total selection gain is employed as optimization criterion: almost all of the

budget is then spent on the cheap evaluation of the lines *per se*. As a consequence, the gain in GCA for the highly heritable component traits increases (due to the indirect selection) while the gain in GCA for grain yield decreases markedly despite the much larger relative economic value assigned to yield. This, however, is in sharp contrast to the goals of practical hybrid rye breeding.

Table 4.1. Optimum allocation and expected selection gain of breeding schemes CYC1_11 and DHL1_11 assuming a minimum number of candidates (N_{LP_MIN}) at the first selection stage (for further abbreviations see Table 3.1)

Scheme N_{LP_MIN}	Selection stage	Optimum allocation			G_VAL		G_GCA_{GY}	
		N	T	L	abs.	[%]	abs.	[%]
CYC1_11	LP	2683	-	3				
no restriction	GCA_1	188	1	4	0.156	100	4.69	100
	GCA_2	21	3	11				
CYC1_11	LP	5006	-	2				
N_{LP_MIN} = 5000	GCA_1	145	1	4	0.156	100	4.46	95.1
	GCA_2	18	3	9				
DHL1_11	LP	937	-	3				
no restriction	GCA_1	125	1	5	0.168	107.7	5.06	107.9
	GCA_2	18	3	11				
DHL1_11	LP	1751	-	2				
N_{LP_MIN} = 1750	GCA_1	74	1	5	0.165	105.8	4.44	94.7
	GCA_2	13	2	9				

4.1.4 Formulae employed to compute the expected gain from selection

In the present study, the exact formulae of Cochran (1951) respectively Utz (1969) have been employed to calculate the gain from multi-stage selection (see Sections 2.2 and 7.2). As these formulae are computationally rather demanding, Utz (1984) derived approximations in which the gain from multi-stage selection is predicted by adding the gains from single-stage selection over stages. The reductions of the genetic variance and of the correlation between selection and gain criterion after each stage of selection are taken into account in the approximations whereas the increasing skewness of the distribution of phenotypic and genotypic values is neglected.

The approximations of Utz (1984) have additionally been implemented for the present study to investigate if the two approaches yield different results. The optimum allocation of resources and the expected selection gain determined with either approach are practically identical for the standard scheme CYC1_11 in which testcross selection is carried out at two successive stages (**Table 4.2**). For scheme CYC1_21, which employs three stages of testcross selection, the optimum allocations also differ only slightly. Using the approximations, the optimum number of BC_1L-testcrosses in the pre-test is higher whereas the number of BC_1L-testcrosses re-evaluated in the main test is smaller than the optimum number obtained with the exact formulae. The expected selection gain of scheme CYC1_21 is underestimated by 2 % (Table 4.2). Checking numerical results of Utz (1969) with the above approximations also revealed an underestimation of the expected gain from three-stage selection in the range of 2 % while the approximate gains from two-stage selection were generally accurate (data not shown).

Table 4.2. Optimum allocation and expected selection gain of schemes CYC1_11 and CYC1_21 employing exact *vs.* approximate formulae to calculate the gain from multi-stage selection in the optimization procedure (for abbreviations see Table 3.1)

Scheme Formulae	Selection stage	Optimum allocation			G_VAL		G_GCA_{GY}	
		N	T	L	abs.	[%]	abs.	[%]
CYC1_11	LP	2683	-	3				
exact	GCA_1	188	1	4	0.1564	100	4.69	100
	GCA_2	21	3	11				
CYC1_11	LP	2753	-	3				
approximate	GCA_1	189	1	4	0.1558	99.6	4.67	99.6
	GCA_2	20	3	11				
CYC1_21	LP	2816	-	3				
exact	GCA_11	206	1	3	0.1469	93.9	4.45	94.9
	GCA_12	42	1	6				
	GCA_2	15	3	13				
CYC1_21	LP	2816	-	3				
approximate	GCA_11	216	1	3	0.1439	92	4.36	93
	GCA_12	29	1	6				
	GCA_2	15	3	13				

Computation times are drastically reduced by employing the approximations of Utz (1984). In the present study, the time needed to determine the selection gain for a single combination of the allocation parameters using the exact formulae was ~1/100 s. Using the approximations, the computation time needed for this purpose is reduced to ~1/10,000 s. This means that if, for example, 200,000 possible combinations are checked during the optimization procedure, the total computation time still stays below one minute. Moreover, the foregoing approximations are much simpler to implement. Thus, they are very useful as long as comparisons between breeding schemes employing different numbers of selection stages are avoided.

4.2 Discussion of the results

4.2.1 Parameters determining the efficiency of a breeding scheme

Large differences in efficiency exist among the alternative breeding schemes investigated. The optimization results show that the efficiency of a breeding scheme mainly depends on three factors which are interdependent to a certain extent: the genotypic variance among the test units, the expenses per candidate, and the length of the breeding scheme.

The **genotypic variance among the test units** increases with higher inbreeding coefficients resp. higher coefficients of coancestry between two random individuals of the candidate lines. From this point of view, test units in later selfing resp. backcrossing generations should be employed. However, additional steps of inbreeding and backcrossing increase the cycle length of a breeding scheme. Moreover, a lot of effort is put into the advancement of candidates that are not worth being continued. Scheme DHL1_11 offers higher variances among the test units than the standard scheme without the foregoing disadvantages. The additive variance among DHL *per se* is 33 % higher than that among S_2L (see Table 2.2). Using DHL to produce the CMS analogues increases the variance among the BC_1L- resp. the BC_2L-testcrosses by 8 % resp. 5 % compared to the standard approach. However, CMS analogues in such early backcrossing generations still contain a considerable proportion of the genome contributed by the donor of the CMS-inducing cytoplasm. With respect to testcross evaluation an even bigger advantage can thus be gained with scheme GAM1_11. Since in this scheme the candidates themselves are evaluated instead of their CMS analogues, the testcross variances at the first and second evaluation stage are increased by 30 % resp. 22 % compared to the standard scheme (see Table 2.2).

Theoretical comparisons of alternative RS methods in barley (Strahwald, 1988), pearl millet (Schipprack, 1993) and sugar beet (Borchardt, 1995) corroborate the foregoing statements regarding the use of test units in later selfing generations. In barley, for example, selection among F_3-plant-derived bulks is more efficient than selection among F_2-plant-derived bulks, though the cycle length is increased by one year. Selection among F_4-plant-derived bulks, however, is less efficient again, as the disadvantage of the additional year overcompensates the advantage of higher variances among the test units (Strahwald, 1988). Based on general expressions for the expected genetic advance, Goldringer *et al.* (1996) investigated the efficiency of several RS methods to improve the line value of a population of self-pollinated crops. Despite the increased cycle length, S_2 family selection was always superior to S_1 family selection. Selection between DHL was the most efficient method, even if another year was required. However, the costs of the different RS methods are neglected in their study. Moreover, the individual methods are not compared under their individual optimum conditions but under the assumption of a fixed selection and evaluation intensity. The results may therefore be misleading.

Under the restriction of a fixed budget, as applied in this study, the **expenses per candidate** determine the overall selection intensity and, to a lesser extent, the evaluation intensity. The higher the costs of producing the test units, the fewer candidates can of course be evaluated. If optimization was carried out on a per-cycle rather than on a per-year basis, the best strategy would thus be to keep the expenses per candidate low by (i) avoiding expensive breeding equipment or techniques and (ii) by postponing the further development of the candidates until a positive selection decision has been reached. Expressed on a per-cycle basis, the selection gain of the cost-intensive scheme DHL1_11, for example, is only 97 % of the optimum standard variant of scheme CYC1_11 while that of the cost-extensive scheme POP2_11 is 102 % (see Table 3.1). On a per-year basis, however, DHL1_11 is superior to POP2_11 by 24 % since the shorter breeding cycle and higher variances among the test units overcompensate the lower number of candidates by far.

As was already demonstrated by the foregoing example, the **cycle length** has a predominant impact on the relative efficiency of the breeding schemes studied. Employing an additional stage of testcross progeny evaluation, for example, is only advantageous if the scheme is not prolonged hereby (see Section 3.2). Shortening the length of a breeding scheme, e.g. by advancing materials in greenhouse programs, causes a strong increase in efficiency despite

increased expenses per candidate and hence reduced numbers of test units (see Section 3.2). Strahwald (1988) obtained similar results with respect to the use of off-season generations to shorten RS procedures in spring barley.

Employing a faster scheme, a breeder will have new lines and experimental hybrids available earlier resulting in an advantage over the competitors with respect to the registration of new varieties. On the long term the advantage of a shorter breeding cycle may become even larger since the recurrent improvement of the base population will also be sped up and progress in variety development is known to be proportional to progress in the base population(s) (Sprague and Eberhart, 1977).

4.2.2 Stability and reliability of the optimization results

Quantitative-genetic parameters may vary among breeding populations and are also subject to changes over time. In maize, for example, Fountain and Hallauer (1996) observed marked differences among three different F_2-populations as well as among different broad-base synthetic populations regarding the genotypic variance for grain yield and many other traits. Economic parameters may also differ among breeding companies and / or breeding programs. Deviations in the quantitative-genetic and economic parameters underlying the present model calculations alter the optimum dimensioning of the schemes as well as the absolute magnitude of the expected selection gain (see Section 3.3). In most of the different variants studied, the relative efficiency of the breeding schemes is also changed to some extent (Table 7.1 in Appendix). However, the ranking of the schemes is never altered by changes in the foregoing parameters. It can thus be concluded that the relative merits of the investigated schemes are constant over a wide range of genetical and economical situations.

Among the **quantitative-genetic parameters**, the size of the dominance variance, the error variance, and the genotype x environment-interaction (G x E) variances markedly influence the optimum allocation of resources (see Section 3.3.1). Knowledge of these parameters is thus crucial for the breeder to optimize the dimensioning of a breeding scheme. The higher the relative size of the **dominance variance**, the more testers have to be employed (at the expense of the number of candidates and locations) to reduce the masking SCA variance among the testcrosses. Despite this adjustment, the expected selection gain decreases. The decrease is severest for grain yield since the ratio of additive to dominance variance is already 2:1 for this trait under standard assumptions and is much wider for the other component traits (see Table 2.3). With increasing **error variances** and / or **G x E variances**, fewer candidates

are evaluated at a larger number of locations to account for the reduction of the heritability. With more accurate trials (i.e. lower error variances), one would expect a decrease in the number of locations. Such a decrease was not observed, however (except for scheme GAM1_11). The reason for this is that the impact of the G x E variances is much larger than that of the error variances. A certain 'minimum' number of locations thus has to be employed to reduce the proportion of variance caused by genotype x environment interaction. In contrast to the foregoing parameters, the amount of **genotypic variance** available in the base population has a strong impact on the absolute magnitude of the expected selection gain, but hardly affects the optimum allocation of a breeding scheme (see Table 3.4). The reason for this is that only the ratio of the genotypic to the error variance is changed under the present assumptions, whereas the ratio of additive to dominance variance and of genotypic to G x E variance remain unchanged. If the genotypic variance is assumed to be low, the error variance becomes thus very important so that more locations are employed as a consequence.

The foregoing findings are corroborated by Borchardt (1995). When comparing alternative methods of pollen-parent line development in sugar beet breeding by model calculations, he also found a larger optimum number of testers for increased amounts of dominance variance. The optimum numbers were lower than those obtained in the present study, however, since the relative size of dominance variance assumed was lower. The influence of the error and G x E variance on the optimum allocation of a breeding scheme were similar in his study.

Among the **economic parameters** studied, the weight put on the **improvement of line performance *versus* GCA** determines the optimum number of candidates for assessing line resp. testcross performance (see Section 3.3.2). The more emphasis is put on GCA, the more testcross progenies are evaluated at the expense of line *per se* evaluation. The optimum numbers of testers and locations are hardly affected, however. The **relative economic value (REV) assigned to grain yield** in the selection index for testcross performance is of rather little influence on the optimum allocation. With a smaller REV for grain yield, fewer testers are employed - hence more candidates can be evaluated. Increasing the REV for grain yield above the standard value assumed hardly alters the optimum allocation of resources. This indicates that the optimum allocation of the standard variant is already dominated by the yield parameters since this trait shows by far the largest amount of dominance variance as well as the highest G x E and error variances. Assuming different REV for grain yield, the expected selection gains in grain yield and the other component traits are of course markedly changed due to the differing index weights.

Both the optimum allocation of resources and the achievable selection gain strongly depend on the available **budget**. Above all, the optimum number of candidates at all evaluation stages is augmented with increasing budget, but the number of testers and locations also gradually increases (see Section 3.3.2). Over the range of budgets studied (€ 100,000 to € 400,000) the ranking of the breeding schemes remains unchanged. The differences in efficiency among the schemes, and thus also the superiority of the best over the worst scheme, are larger for higher budgets. This was also found by Strahwald (1988) in barley, Schipprack (1993) in pearl millet (both authors varied the annual labour capacity instead of the budget), and Borchardt (1995) in sugar beet. The return on investment is rather low for all the breeding schemes studied: doubling the available budget only causes a 10-13 % increase in the expected selection gain. Interestingly, choosing a more efficient scheme often leads to a markedly higher increase in efficiency than employing a considerably higher budget for a less efficient method (see Fig. 3.1). This result impressively stresses the importance of optimizing breeding schemes with respect to their genetical, technical, and economical aspects.

To investigate if the selection gain expected from the model calculations is of realistic size, it is to be compared with the average realized selection gain in hybrid rye breeding. Comparing seven hybrid varieties released in Germany during 1995-1999 with two older hybrid varieties with respect to their performance in the official trials during 1993-1997, the average yearly progress in hybrid breeding was estimated. Assuming that the progress in the hybrid varieties is roughly twice the progress in GCA in either of the two parents (Falconer and Mackay, 1996), estimates of the average realized gain in GCA per year were obtained (**Table 4.3**). Since neither the breeding scheme(s) employed nor the budget spent on the development of the foregoing hybrid varieties are known, a comparison of these figures with the gains expected from the model calculations can of course only indicate how close the optimization results are to reality. For grain yield, the gain in GCA per year expected from the optimum standard variant of scheme CYC1_11 (4.69 g m^{-2} $yr.^{-1}$) is very similar to the average realized gain in hybrid breeding (4 g m^{-2} $yr.^{-1}$ with a range of 2 to 5 g m^{-2} $yr.^{-1}$ for the different hybrid varieties; Table 4.3). The same is true for thousand-kernel weight. For plant height and falling number, the expected gains lie at the upper border of the range of realized gains determined (-0.42 cm $yr.^{-1}$ for plant height resp. 2.2 s $yr.^{-1}$ for falling number). For lodging resistance and leaf rust resistance, the expected gains seem to be somewhat overestimated. This may be explained by the fact that in the registration of hybrid rye varieties the main focus is on grain yield while a slight weakness e.g. in lodging resistance might be tolerated (Wilde, pers.

comm.). On the whole, the expected gains are thus in good agreement with selection gains presently realized in hybrid rye breeding indicating also that realistic budgets were assumed in the present study.

Table 4.3. Comparison of the yearly selection gain in GCA (G_GCA) expected from the optimum standard variant of scheme CYC1_11 with the average realized gain in hybrid rye breeding for all traits under study (GY = grain yield, PH = plant height, LR = lodging resistance, TKW = thousand-kernel weight, FN = falling number, LRR = leaf rust resistance)

G_GCA	GY [g m^{-2}]	PH [cm]	LR [score]	TKW [g]	FN [s]	LRR [score]
Expected[1]	4.69	-0.41	-0.10	0.14	1.71	-0.04
Realized	4.00	-0.22	-0.03	0.18	0.98	-0.02

[1] Selection gains for all traits except grain yield are total gains, i.e. the sum of the direct gain in GCA plus the indirect gain in GCA resulting from selection on line performance (see Section 4.1.3)

4.2.3 Valuation of the breeding schemes and consequences of the results for practical breeding programs

Employing the standard scheme **CYC1_11** with a cycle length of eleven years, selection gains similar to those presently realized in hybrid rye breeding can be expected (see above). Since all breeding steps involved are carried out in the field, the levels of organizational skills and cost-intensive technical facilities required are comparatively low. This is a clear advantage from a practical point of view since the technical simplicity and security of a scheme are of great importance for practical breeding programs with large numbers of entries.

The relative efficiency of CYC1_11 can be markedly increased (+ ~7 %) if its cycle length is reduced to ten years by producing the BC_0 and BC_1L of all selected S_2L in a single year (see Section 3.2). Among the conventional breeding schemes investigated ('conventional' meaning without using DHL or gametocides), this variant shows by far the highest efficiency which comes close to that of scheme DHL1_11. Two generations per year in winter rye can only be achieved in the greenhouse with prior artificial vernalization (≥ 8 wk.), however. Off-season nurseries like in spring barley or maize are not possible. The technical simplicity and security of this variant are thus lower than for the standard variant. If the greenhouse generation fails, for example, a whole year is lost and the expected selection gain is reduced to only 97 % of the optimum standard variant. A breeder must thus weigh the foregoing advantages and disadvantages thoroughly to decide if this variant is appropriate.

Scheme **CYC1_21** differs from the standard scheme only by an additional stage of BC_1L-testcross selection. It is also a technically rather simple and secure scheme. With respect to the expected selection gain, scheme CYC1_21 is only superior to the standard scheme if the additional evaluation stage doesn't increase the cycle length above eleven years (see Section 3.2). However, employing a pre- and a main test instead of a single testing stage improves the reliability of the evaluation procedure and thus of the selection decision. This aspect could not be considered in the efficiency criterion. From a breeder's point of view, an additional selection stage may thus still be worthwile even if this requires an extra year.

As in the present study, evaluating S_1L, S_2L or DHL at two successive stages proved only advantageous for the recurrent development of pollen-parent lines in sugar beet when the cycle length was not increased hereby (Borchardt, 1995). Similar results were obtained by Schipprack (1993) in pearl millet who found that the disadvantage of an increased cycle length outweighs the advantage of an additional stage of S_1L or S_2L evaluation. In contrast, Strahwald (1988) in barley found two-stage evaluation of the test units usually more efficient than single-stage evaluation despite the increased cycle length.

Scheme **POP2_11** shows the lowest relative efficiency of the breeding schemes investigated due to its long duration of 13 years. However, a certain part of a breeder's efforts has to be devoted to genetically broadened base populations (e.g. crosses between second cycle materials and open-pollinated varieties) to ensure sufficient genetic variability in the breeding material and thus continued progress from selection on a long term. Assuming that the additive genetic variance is higher in such genetically broader populations than in second cycle material (Hallauer and Miranda, 1981), the selection gain expected from scheme POP2_11 increases. Assuming e.g. 25 % higher additive variances for all traits of interest, the relative efficiency of POP2_11 is 99 % of the optimum standard variant despite the longer breeding cycle (**Table 4.4**). With 50 % higher additive variances, scheme POP2_11 would even be superior to the standard scheme by 10 %. The usefulness of a base population, however, depends not only on its genetic variance and the selection gain resulting therefrom, but also on the population mean (Schnell, 1983). With respect to line *per se* performance, the mean of genetically broader populations will usually be much lower than that of second cycle populations. Yet, with regard to combining ability the difference is not necessarily that large. Even for grain yield, Miedaner and Geiger (1998) observed rather small differences between the combining abilities of five BC_2-lines derived from various exotic genetic materials and an

elite inbred line. Under these circumstances the development of inbred lines from broader based populations can thus be competitive and should not be neglected.

Table 4.4. Influence of the amount of additive variance available in the base population on the expected selection gain of scheme POP2_11 relative to that of the standard scheme under standard assumptions (for abbreviations see Table 3.1)

Additive variance	Selection stage	Optimum allocation				G_VAL		G_GCA$_{GY}$	
		N	T	L		abs.	[%]	abs.	[%]
100 %	LP_1	3816	-	1					
(= Standard)	LP_2	1091	-	3		0.135	86.5	3.90	83.2
	GCA_1	180	1	4	2				
	GCA_2	21	3	11	2				
125 %	LP_1	3744	-	1					
	LP_2	1064	-	3		0.154	98.7	4.51	96.2
	GCA_1	189	1	4	2				
	GCA_2	20	3	11	2				
150 %	LP_1	3934	-	1					
	LP_2	1095	-	3		0.171	109.6	5.02	107
	GCA_1	198	1	4	2				
	GCA_2	21	2	12	2				

The expected selection gain per year of scheme **DHL1_11** is more than 7 % higher than that of CYC1_11. However, at present DHL production in rye is strongly limited by enormous genotypic differences in anther culture ability (Deimling and Geiger, 1996). Other haploid techniques such as *in vivo* haploid induction by interspecific pollination have not been developed so far. Schemes employing DHL can therefore not be used as a breeding routine yet. Scheme DHL1_11 is cost-intensive and technically very demanding. A tissue culture laboratory is needed in addition to a fully climate-controlled greenhouse. Failures in DHL production or in developing the BC_0 and BC_1 in one year in the greenhouse would result in an increased cycle length and thus in a relative efficiency below that of the standard scheme. In contrast to variety development in self-pollinated crops or line development in hybrid maize breeding, little time is saved by the DH approach because CMS analogues need to be developed. Another disadvantage of DHL1_11 is the low overall selection intensity since only rather few candidates enter the evaluation process. This number might be too low to allow the selection of lines which meet the minimum standards required in all the traits of interest (see

Section 4.1.3). Almost the same efficiency as with DHL1_11 can be reached by employing the short variant of CYC1_11 (see above). However, the technical security of the latter is higher. The use of scheme DHL1_11 can thus not be recommended for practical breeding programs at present.

Similar results were obtained by Borchardt (1995). In his study, a breeding scheme employing DHL was slightly superior to the best conventional scheme with respect to RS, but not with respect to line development. Wilde (1996) also 'doubts that the DHL technique becomes a widely used tool in practical hybrid rye breeding' due to the genotypic limitations for anther culture response and the costs of DHL production. In winter barley, Strahwald (1988) found DHL selection to be inferior to combined selection on F_1-bulks and F_3-plant-derived bulks despite a shorter breeding cycle of the DHL scheme. In spring barley, DHL selection proved superior to conventional methods as long as its cycle length was shorter. If one or two off-season generations were employed, however, the conventional methods showed a higher efficiency. In contrast to this, Goldringer *et al.* (1996, 1997) found a general superiority of RS schemes employing DHL over conventional methods. However, since no costs were taken into account in their studies, only the genetical advantages of the DHL method are considered while the operational and economical disadvantages are neglected.

By far the highest efficiency of all breeding schemes investigated is expected from scheme **GAM1_11**. On a per-year basis, GAM1_11 is 31 % superior to the standard scheme. Ignoring its two years shorter cycle length, the relative efficiency of GAM1_11 on a per-cycle basis is still 107 % due to the much higher variances among the testcross progenies and the rather low expenses per candidate resulting from the postponed development of CMS analogues. Unfortunately, there is no suitable gametocide available for rye so far so that such a scheme can not be used at present. However, a similar efficiency as with the gametocide approach would be expected if CMS-testers were available which represent the pollinator pool. The development of such testers is principally possible though not easy since besides the major restorer genes a number of minor restorer genes exist (Miedaner *et al.*, 1997) which would all have to be eliminated or suppressed. To date, no reports on a successful use of this approach have been published. Nevertheless, the high selection gains expected from scheme GAM1_11 may encourage breeders to develop such testers despite the efforts and costs involved. Another possible approach could be the development of a second seed-parent pool which is not related to the actual seed-parent material. Existent CMS lines from either of these pools

could then be used as testers for candidate lines of the other pool to allow a preselection for combining ability before the conversion into CMS analogues is started. The success of such an approach would of course depend on the extent to which combining ability to the second seed-parent pool reflects combining ability to the pollinator pool, the ultimate goal of selection.

The results obtained from the model calculations have some consequences with respect to the **optimum allocation of practical breeding programs**. According to the optimization results, only one tester should be used at the first stage of testcrossing and only rather few testers at the second testcrossing stage assuming standard genetic variances. Yet, employing more than one **tester** from the beginning reduces the risk of a complete loss of testcross seed (e.g. caused by different flowering dates of a candidate line and the tester) and thus increases the technical security of the scheme. Moreover, with only one tester the breeder runs the risk of getting a differentiation among the candidate lines that is specific for the tester employed. In addition to this, it will generally be difficult to find testers that ensure a good differentiation among the candidate lines for all the traits under selection. Using two testers at the first testcrossing stage is mandatory if dominance variances are high (see Section 3.4). It detracts little from the expected selection gain if the relative size of dominance variance is assumed to be average or even low (see Section 3.4). A minimum of two testers at the first testcrossing stage is thus highly recommended for practical breeding programs. This recommendation is in agreement with Wilde (1996). At the second testcrossing stage, the number of testers employed should also be slightly larger than suggested by the optimization results.

The relative size of dominance variance increases with increasing frequency of the favourable allele. Assuming e.g. complete dominance, the ratio of dominance to additive variance is 0.5 for a frequency of the favourable allele of $p = 0.5$, 1.17 for $p = 0.7$, and 2.0 for $p = 0.8$ (Falconer and Mackay, 1996). As a consequence, larger proportions of dominance variance have to be expected in advanced breeding materials. The breeder should thus make sure that a sufficient number of testers is employed to assess combining ability in such materials.

The optimum number of **locations** at the last evaluation stage suggested by the optimization results is very high for all breeding schemes studied. Employing fewer locations at this stage, however, doesn't reduce the expected selection gain markedly as long as five or six locations are used (see Section 3.4). It will thus be a good strategy for practical breeders to employ only five or six locations at the last evaluation stage and increase the numbers of candidates and

testers instead. If genotype x environment interaction variances are very large, the number of locations might have to be corrected upwards.

In the future, selling hybrid rye in Eastern European countries will become increasingly important (Wilde und Sepstrup, 1999). The challenge facing hybrid rye breeders will thus be to develop excellent varieties for an ecologically broader target area of environments than ever before. If a breeder should develop varieties adapted to specific environmental conditions in separate breeding programs or rather aim at genotypes adapted to the whole range of environments by employing a single breeding program essentially depends on the importance of genotype x environment interaction (G x E). Employing separate breeding programs becomes the more efficient the higher the importance of G x E (see Section 3.3.1) and the higher the amount of available resources (Wilde und Sepstrup, 1999).

5 Summary

The importance of hybrid rye - and thus also of hybrid rye breeding - has steadily increased over the last decades. Hybrid varieties show a superior grain yield and are more uniform than open-pollinated varieties. Both aspects make hybrid varieties highly attractive for the grower. In hybrid rye breeding, seed-parent and pollinator lines are developed from two genetically divergent gene pools. Inbred line development comprises two major phases: selection for line performance *per se* followed by selection for combining ability to the respective opposite gene pool. Cytoplasmic-genic male sterility (CMS) is employed as hybridizing mechanism.

The present study deals with model calculations aiming at the optimization and comparison of alternative schemes of seed-parent line development in hybrid rye breeding on the basis of their expected selection gain per year. Five breeding schemes were investigated which differ in the basic genetic material assumed, in the type of test units as well as the number of selection stages for line and testcross selection, and in the cycle length. The scheme defined as a standard employs second cycle material. First, S_2-lines are evaluated *per se*. Selection for combining ability is then carried out at two successive stages employing testcross progenies of the CMS analogues of the candidate lines in backcross generations BC_1 resp. BC_2. The length of the standard scheme is eleven years. The first alternative scheme differs from the standard scheme by an additional stage of BC_1L-testcross selection. The second alternative scheme is especially suited for the development of seed-parent lines from broader-based population material. In addition to these conventional methods, a scheme using doubled haploid lines (DHL) was investigated as well as a scheme in which the testcross progenies are produced by means of a gametocide instead of CMS.

The breeding schemes were optimized for the number of candidates, testers to assess testcross performance, test locations, and replicates at the individual selection stages. To determine the optimum allocation and the expected selection gain, computer programs were developed using the C++ programming language.

The selection criterion employed in the model calculations is an index that comprises plant height, thousand-kernel weight, and resistance to lodging, pre-harvest sprouting, and leaf rust when selecting for line performance. In testcross evaluation, the index additionally comprises grain yield as the most important trait. The criterion used to optimize and compare the breeding schemes is the sum of the selection gains per year in line performance and general combining ability (GCA) weighed in the ratio of 1 : 3. Prediction of the selection gains was

based on current estimates of the relevant quantitative-genetic and economic parameters obtained from data provided by German hybrid rye breeders. Optimization was carried out under the restriction of a fixed available budget of € 200,000 per year for each breeding scheme. The number of finally selected lines was set to three. All schemes were first optimized *per se* and the optimized versions compared afterwards.

With respect to the optimum allocation of resources, the alternative schemes mainly differ in the number of candidates at the individual selection stages. In the standard scheme, 2700 S_2-lines are evaluated *per se* at three locations. The best 188 candidates are selected and CMS analogues of them developed. The BC_1-lines are crossed to one tester and the testcrosses are evaluated at four locations with two replicates. Testcross progenies of the 21 best BC_2-lines with three testers are finally evaluated at eleven locations with two replicates. For the DHL-scheme, the numbers of candidates at all selection stages are much lower. For the scheme employing a gametocide, line evaluation is less intense. A much higher number of candidates enter testcross evaluation instead.

The influence of changes in the underlying quantitative-genetic and economic parameters on the optimum allocation and relative efficiency of the breeding schemes was investigated in the present study. The amount of genotypic variance in the base population strongly influences the expected selection gain but hardly affects the optimum allocation. The higher the relative size of the dominance variance, the more testers have to be employed (at the expense of the number of candidates and locations) to reduce the masking SCA variance among the testcrosses. Despite this adjustment, the expected selection gain decreases clearly. With increasing error variances and / or genotype x environment-interaction variances, fewer candidates are evaluated at a larger number of locations to account for the reduction of the heritability. With increasing budget the optimum number of candidates at all evaluation stages increases. The number of testers and locations also increases gradually but is clearly less affected. Over the range of budgets investigated the return on investment is rather low for all schemes: doubling the budget only causes a 10-13 % increase in the expected selection gain. Results show that choosing a more efficient scheme often leads to a stronger increase in the selection gain than employing a considerably larger budget for a less efficient scheme.
The ranking of the alternative breeding schemes was never altered by changes in the foregoing parameters. It can thus be concluded that the relative merits of the investigated schemes remain constant over a wide range of genetical and economical situations.

The optimized breeding schemes differ markedly in their expected selection gain per year. By far the highest efficiency is expected from the scheme employing a gametocide instead of CMS to produce the testcross progenies. It is 31 % superior to the standard scheme (that was set to 100 %) due to the larger genotypic variances among the testcross progenies and the two years shorter breeding cycle. The DHL-scheme is 8 % superior to the standard scheme. Unfortunately, none of these two approaches can be used as a routine in rye breeding at present. Yet, the development of CMS-testers representing the pollinator gene pool should enable a similar progress as the use of gametocides and may thus be worth the costs and efforts involved. Almost the same efficiency as with the DHL-scheme can be reached with a short variant of the standard scheme (107 %) whose cycle length is reduced to ten years by producing an off-season generation in the greenhouse. Employing an additional stage of BC_1L-testcross selection with the standard scheme is only advantageous if the cycle length is not prolonged hereby. Otherwise the extra year reduces the relative efficiency of this scheme to 94 %. The scheme for population material shows the lowest relative efficiency (86 %) due to its long duration of 13 years. If one assumes that the additive genetic variance is 30-50 % larger in genetically broader populations than in second cycle material, this scheme becomes competitive with the standard scheme, however.
For practical breeders, the suitability of a breeding scheme may depend on additional criteria like the simplicity of operation or the demand for cost-intensive technical equipment. Such aspects are discussed for the schemes investigated.

The results obtained have some consequences regarding the optimum allocation of practical breeding programs. According to the optimization results, only one tester should be used at the first testcrossing stage except if dominance variances are very high. Yet, employing two testers instead hardly affects the expected selection gain but increases the security of testcross seed production. It is therefore strongly recommended for practical breeding programs. Assuming a limited number of test locations, the expected selection gain is not severely reduced as long as five or six locations are employed at the final selection stage.

All in all, the studies underline the great significance of model calculations for optimizing breeding methods.

Zusammenfassung

Die Bedeutung von Hybridroggen ist in den letzten Jahrzehnten beständig angestiegen – und damit auch die Bedeutung der Hybridroggenzüchtung. Hybridsorten zeigen überlegene Erträge und sind zudem homogener als offenbestäubte Sorten. Dies macht Hybridsorten für den Landwirt sehr attraktiv. In der Hybridroggenzüchtung werden Saat- und Pollenelterlinien aus zwei genetisch divergenten Formenkreisen entwickelt. Die Inzuchtlinienentwicklung umfaßt zwei Phasen: die Selektion auf Linieneigenleistung gefolgt von der Selektion auf Kombinationsfähigkeit zum jeweils anderen Formenkreis. Als Hybridmechanismus dient die cytoplasmatisch-genische männliche Sterilität (CMS).

Gegenstand der vorliegenden Arbeit sind Modellrechnungen zur Optimierung und Bewertung alternativer Schemata der Saatelterlinienentwicklung in der Hybridroggenzüchtung anhand ihres erwarteten Selektionsgewinns pro Jahr. Untersucht wurden fünf Zuchtschemata, die sich bezüglich des Ausgangsmaterials, der Art der Testeinheiten, der Anzahl der Selektionsstufen und der Dauer unterscheiden. Als Standard wurde ein Second-Cycle-Schema definiert, in dem zunächst einstufig auf die Eigenleistung von S_2-Linien selektiert wird. Die Selektion auf Kombinationsfähigkeit erfolgt dann in zwei aufeinanderfolgenden Stufen. Als Testeinheiten dienen Testkreuzungsnachkommenschaften der CMS-Analogformen der Kandidatenlinien in Rückkreuzungsgeneration BC_1 bzw. BC_2. Die Länge des Standardschemas beträgt elf Jahre. Das erste alternative Schema unterscheidet sich vom Standardschema durch eine zusätzliche Stufe der BC_1L-Testkreuzungsselektion. Das zweite alternative Schema ist besonders geeignet zur Entwicklung von Saatelterlinien aus genetisch breiterem Populationsmaterial. Neben diesen konventionellen Verfahren wurde die Verwendung von doppelhaploiden Linien (DHL) untersucht sowie ein Schema, in dem die Testkreuzungen mit Hilfe eines Gametozids anstelle der CMS erstellt werden.

Für die Zuchtschemata wurde die optimale Anzahl der Kandidaten, der Tester zur Erstellung der Testkreuzungsnachkommenschaften, der Prüforte und der Wiederholungen auf allen Selektionsstufen ermittelt. Zur Bestimmung der optimalen Allokation und des erwarteten Selektionsgewinns wurden Computerprogramme in der Programmiersprache C++ entwickelt.

Als Selektionskriterium dient in den Modellrechnungen ein Selektionsindex, welcher für die Selektion auf Eigenleistung die Merkmale Wuchshöhe, Lager bei Reife, Tausendkorngewicht, Fallzahl und Braunrostresistenz umfaßt. Wird auf Kombinationsfähigkeit selektiert, so beinhaltet der Index zusätzlich den Kornertrag als wichtigstes Merkmal. Als Optimierungs-

und Vergleichskriterium dient die Summe der erwarteten Selektionsgewinne in Eigenleistung und Allgemeiner Kombinationsfähigkeit (GCA) gewichtet im Verhältnis von 1 : 3. Die Vorhersage der Selektionsgewinne basiert auf aktuellen Schätzwerten der hierfür relevanten quantitativ-genetischen und ökonomischen Parameter, die aus Daten deutscher Hybridroggenzüchter gewonnen wurden. Die Optimierung wurde unter der Restriktion eines begrenzten Jahresbudgets von standardmäßig 200.000 € für jedes Schema durchgeführt. Die Anzahl der endgültig selektierten Linien wurde auf drei festgesetzt. Alle Schemata wurden zunächst in sich optimiert und die optimierten Versionen anschließend miteinander verglichen.

In Bezug auf die optimale Dimensionierung unterscheiden sich die Schemata hauptsächlich in der Anzahl der Kandidaten auf den einzelnen Selektionsstufen. Im Standardschema werden zunächst 2700 S_2-Linien an drei Orten auf ihre Eigenleistung geprüft. Die besten 188 Kandidaten werden ausgewählt und in das CMS-induzierende Cytoplasma eingelagert. Die BC_1-Linien werden dann mit einem Tester gekreuzt. Die Testkreuzungsnachkommenschaften werden an drei Orten in zwei Wiederholungen geprüft. Testkreuzungen der 21 besten BC_2-Linien mit drei Testern werden abschließend an elf Orten in zwei Wiederholungen evaluiert. Für das DHL-Schema sind die Kandidatenzahlen auf allen Selektionsstufen erheblich niedriger. Im Gametozid-Schema wird weniger intensiv auf Eigenleistung geprüft, dafür ist die Anzahl der Kandidaten im ersten GCA-Test deutlich erhöht.

Der Einfluß veränderter quantitativ-genetischer und ökonomischer Parameter auf die optimale Dimensionierung und die relative Vorzüglichkeit der alternativen Schemata wurde in dieser Studie ebenfalls untersucht. Die Höhe der genotypischen Varianz in der Ausgangspopulation beeinflußt den erwarteten Selektionsgewinn deutlich, verursacht jedoch kaum Änderungen in der optimalen Allokation. Mit höherer Dominanzvarianz müssen mehr Tester verwendet werden, um die maskierende SCA-Varianz zwischen den Testkreuzungen zu verringern. Dies geht zu Lasten der Anzahl der Kandidaten und Prüforte, so daß der Selektionsgewinn deutlich abnimmt. Mit steigender Fehlervarianz und / oder Genotyp x Umwelt-Interaktionsvarianzen werden weniger Kandidaten an einer größeren Anzahl von Prüforten evaluiert, um die Verringerung der Heritabilität auszugleichen. Mit steigendem Budget steigt vor allem die Anzahl der Kandidaten auf allen Selektionsstufen. Die Anzahl der Tester und Orte steigt ebenfalls langsam an, ist aber weniger stark verändert. Im untersuchten Budgetbereich liegen alle Schemata im Bereich stark abnehmender Grenzerträge. Eine Verdopplung des Budgets bewirkt lediglich eine Steigerung des erwarteten Selektionsgewinns um 10-13 %. Die Ergebnisse zeigen, daß die Wahl eines effizienteren Schemas oftmals einen erheblich

größeren Fortschritt ermöglicht als eine deutliche Erhöhung des Budgets für ein unterlegenes Verfahren.
Die Rangfolge der untersuchten Zuchtschemata wurde durch Änderungen der vorgenannten Parameter in keinem Fall verändert. Daraus kann der Schluß gezogen werden, daß die relative Vorzüglichkeit der alternativen Schemata für eine Vielzahl genetischer und ökonomischer Situationen konstant ist.

Zwischen den optimierten Zuchtschemata ergaben sich erhebliche Effizienzunterschiede. Den bei weitem höchsten Selektionsgewinn pro Jahr verspricht das Gametozid-Schema. Aufgrund der sehr viel höheren Testkreuzungsvarianzen und der um zwei Jahre kürzeren Dauer ist es dem Standardschema (gleich 100 % gesetzt) um 31 % überlegen. Das DHL-Schema ist dem Standardschema um 8 % überlegen. Beide genannte Verfahren sind allerdings derzeit bei Roggen nicht routinemäßig einsetzbar. Einen ähnlich hohen Fortschritt wie der Einsatz von Gametoziden ließe jedoch die Entwicklung von CMS-Testern im Pollenelter-Formenkreis erhoffen. Diese könnte daher trotz der hiermit verbundenen Anstrengungen und Kosten ein lohnender Ansatz zur Steigerung der Effizienz in der Hybridroggenzüchtung sein. Beinahe die gleiche Effizienz wie mit dem DHL-Schema kann durch eine Verkürzung der Zykluslänge des Standardschemas um ein Jahr durch die Erstellung einer Zwischengeneration im Gewächshaus erreicht werden (107 %). Eine zusätzliche Stufe der Testkreuzungsselektion ist nur vorteilhaft, wenn hierdurch die Länge gegenüber dem Standardschema nicht erhöht wird. Anderenfalls beträgt die Effizienz dieser Variante aufgrund des zusätzlichen Jahres 94 %. Das besonders für Populationsmaterial geeignete Zuchtschema zeigt aufgrund seiner Länge von 13 Jahren die geringste Effizienz (86 %). Nimmt man jedoch an, daß die Additivvarianz in genetisch breiteren Ausgangspopulationen größer ist als in Second-Cycle Material, so wird dieses Schema durchaus konkurrenzfähig zum Standardschema.
Im praktischen Zuchtbetrieb sind für die Wahl geeigneter Zuchtmethoden neben der Effizienz noch andere Kriterien maßgeblich, z.B. die Einfachheit der Durchführung oder der Anspruch an kostenintensive technische Ausstattungen. Diese Aspekte werden in dieser Arbeit für die untersuchten Schemata ebenfalls diskutiert.

Aus den erzielten Ergebnissen lassen sich einige Empfehlungen für die Dimensionierung praktischer Zuchtprogramme ableiten. Den Optimierungsergebnissen zufolge sollte auf der ersten Stufe der Testkreuzungsselektion stets nur ein Tester verwendet werden, sofern nicht die Dominanzvarianz sehr groß ist. Der Einsatz von zwei Testern verringert den erwarteten

Selektionsgewinn jedoch kaum, erhöht aber die technische Sicherheit der Produktion von Testkreuzungssaatgut deutlich und wird daher für praktische Zuchtprogramme empfohlen. Die Annahme einer begrenzten Anzahl von Prüforten führt zu keiner nennenswerten Verringerung des erwarteten Selektionsgewinns, sofern auf der letzten Selektionsstufe noch fünf oder sechs Prüforte zur Verfügung gestellt werden.

Insgesamt unterstreichen die vorliegenden Untersuchungen die große praktische Bedeutung zuchtmethodischer Modellrechnungen.

6 References

Baker, R.J. 1986. Selection indices in plant breeding. CRC Press, Boca Raton, Florida.

Becker, H.C., H.H. Geiger, and K. Morgenstern. 1982. Performance and phenotypic stability of different hybrid types in winter rye. Crop Sci. 22:340-344.

Becker, H.C. and J. Léon. 1988. Stability analysis in plant breeding. Plant Breed. 101:1-23.

Borchardt, D.C. 1995. Optimierung von Methoden zur Züchtung von Zuckerrüben. Diss., Univ. Hohenheim, Stuttgart.

Bulmer, M.G. 1971. The effect of selection on genetic variability. American Naturalist 105:201-211.

Bundessortenamt. 2000. Beschreibende Sortenliste. Landbuch-Verlag. Hannover.

Burrows, P.M. 1972. Expected selection differentials for directional selection. Biometrics 28:1091-1100.

Choo, T.M. and L.W. Kannenberg. 1979. Relative efficiencies of population improvement methods in corn: a simulation study. Crop Sci. 19:179-185.

Cochran, W.G. 1951. Improvement by means of selection. 2nd Berkeley Symp. Math. Stat. Prob. 449-470.

Cockerham, C.C. 1963. Estimation of genetic variances. p. 53-93. *In* C.H. Hanson and H.F. Robinson (eds). Statistical Genetics and Plant Breeding. NAS-NRC 982.

Deimling, S. and H.H. Geiger. 1996. Anther culture in rye: methodical improvements and genetic analysis. Vortr. Pflanzenzüchtg. 35:225-235.

Eberhart, S.A. and W.A. Russell. 1969. Stability parameters for comparing varieties. Crop Sci. 6:36-40.

Erfurt, M.C. 1997. Schätzung der Linieneigenleistung, Kombinationsfähigkeit und Heterosis für quantitative Merkmale bei Winterroggen. Diplomarbeit, Univ. Hohenheim, Stuttgart.

Falconer, D.S. and T.F.C. Mackay. 1996. Introduction to quantitative genetics. 4th Ed., Longman Sci. and Tech., Harlow, UK.

Flehinghaus-Roux, T. 1994. Induktion und Regeneration androgenetischer Pflanzen bei Roggen. Diss., Univ. Hohenheim, Stuttgart.

Fountain, M.O. and A.R. Hallauer. 1996. Genetic variation within maize breeding populations. Crop Sci. 36:26-32.

Fraser, A. and D. Burnell. 1970. Computer models in genetics. McGraw-Hill, New York.

Gallais, A. 1993. Fields of efficiency of breeding methods for *per se* value or combining ability in plant breeding. Agronomie 13:467-480.

Geiger, H.H. 1975. Alternativen der heutigen Roggenzüchtung. Getreide, Mehl und Brot 29:197-202.

Geiger, H.H. 1982. Breeding methods in diploid rye (*Secale cereale* L.). Tag.-Ber., Akad. Landwirtsch.-Wiss. DDR, Berlin, 198:305-332.

Geiger, H.H. 1985. Hybrid breeding in rye (*Secale cereale* L.). p.237-265. *In* Proc. Part I. Eucarpia Meeting of the Cereal Section on Rye. Svalöv, Sweden.

Geiger, H.H. and H.C. Becker. 1984. Epistatic and buffering effects in hybrid rye. Vortr. Pflanzenzüchtg. 7:194-208.

Geiger, H.H. and T. Miedaner. 1999. Hybrid rye and heterosis. p. 439-450. *In* J.G. Coors and S. Pandey (eds.): The Genetics and Exploitation of Heterosis in Crops. ASA-CSSA-SSSA, Madison, Wisc., USA.

Geiger, H.H. and F.W. Schnell. 1970. Cytoplasmic male sterility in rye (*Secale cereale* L.). Crop Sci. 10:590-593.

Geiger, H.H. and A. Tomerius. 1997. Quantitative genetics and optimum breeding plans. p. 15-26. *In* Proc. Meet. of the Eucarpia section 'Biometrics in plant breeding', Poznan, Poland.

Geiger, H.H., A.E. Melchinger, and G. Seitz, 1987. Vorhersage der phänotypischen Stabilität von Dreiweghybriden bei Mais. Vortr. Pflanzenzüchtg. 12:145-155.

Gey, A.-K.M., T. Miedaner, and H.H. Geiger. 1996. Relationship between leaf rust resistance of inbred lines and test crosses in winter rye. Vortr. Pflanzenzüchtg. 35:184-185.

Goldringer, I., P. Brabant, and A. Gallais. 1996. Theoretical comparison of recurrent selection methods for the improvement of self-pollinated crops. Crop Sci. 36:1171-1180.

Goldringer, I., P. Brabant, and A. Gallais. 1997. Theoretical study of the relative efficiency of recurrent selection methods applied to self-pollinated species when epistasis is considered. p. 117-121. *In* Proc. Meet. of the Eucarpia Section 'Biometrics in Plant Breeding', Poznan, Poland.

Górny, A.G., H.H. Geiger, K. Morgenstern, and R.K. Singh. 1982. Correlations between seedling and adult plant characters in hybrids and inbred lines of rye (*Secale cereale* L.). Tag.-Ber., Akad. Landwirtsch.-Wiss. DDR, Berlin, 198:389-399.

Griffing, B. 1956. A generalized treatment of the use of diallel crosses in quantitative inheritance. Heredity 10:31-50.

Grüneberg, W.J. 1993. Mehrstufenselektion in spaltenden Generationen der Selbstbefruchter-züchtung. Diss., Univ. Hannover.

Gupta, S.S. 1963. Probability integrals of multivariate normal and multivariate t. Ann. Math. Stat. 34:792-828.

Hallauer, A.R. and J.B. Miranda. 1981. Quantitative genetics in maize breeding. Iowa State University Press. Ames, Iowa.

Hartmann, A. 1997. Untersuchungen zur genetischen Variation von Winterroggen unter ortsüblicher und verringerter Stickstoffdüngung. Diss., Univ. Hohenheim, Stuttgart.

Hepting, L. 1978. Analyse eines 7 x 7-Sortendiallels zur Ermittlung geeigneten Ausgangsmaterials für die Hybridzüchtung bei Roggen. Z. Pflanzenzüchtg. 80:188-197.

Kempthorne, O. 1957. An introduction to genetics statistics. John Wiley & Sons, New York.

Klinger, S.M. 1985. Untersuchungen zum Frühen Testen auf Kombinationsfähigkeit in der Hybridroggenzüchtung. Diss., Univ. Hohenheim, Stuttgart.

Köhler, K.L. 1986. Experimentelle Untersuchungen zur Aufspaltungsvariation und -kovariation der Linieneigenleistung und Kombinationsfähigkeit bei Roggen. Diss., Univ. Hohenheim, Stuttgart.

Loock, A. 1991. Alternative Verfahren der Rekurrenten Selektion zur Verbesserung der Fallzahl bei Roggen. Diss., Univ. Hohenheim, Stuttgart.

Ludwig, W.F. 1992. Quantitativ-genetische und methodische Untersuchungen zur Züchtung auf Fußkrankheitsresistenz bei Roggen (*Secale cereale* L). Diss., Univ. Hohenheim, Stuttgart.

Lundqvist, A. 1956. Self-incompatibility in rye. I. Genetic control in the diploid. Hereditas 42:293-348.

Madej, L.J. 1996. Worldwide trends in rye growing and breeding. Vortr. Pflanzenzüchtg. 35:1-6.

Mechelke, W. 1981. Die Testkreuzungs-, S_1^2- und S_2-Leistung von S_1-Linien als Selektionskriterium in der Hybridzüchtung bei Winterroggen. Diplomarbeit, Univ. Hohenheim, Stuttgart.

Melchinger, A.E. 1984. Effects of recombination in the parental populations on the means and combining ability variances in hybrid populations of maize (*Zea mays* L.). Diss., Univ. Hohenheim, Stuttgart.

Miedaner, T. und H.H. Geiger. 1998. Chancen und Konzepte der Nutzung genetischer Ressourcen in der Hybridroggenzüchtung. S. 17-22. *In* Bericht über die Arbeitstagung 1998 der Arbeitsgemeinschaft der Saatzuchtleiter in Gumpenstein, Österreich.

Miedaner, T., F. Dreyer, C. Glass, H. Reinbold, und H.H. Geiger. 1997. Kartierung von Genen für die Pollenfertilitätsrestauration bei Roggen (*Secale cereale* L.). Vortr. Pflanzenzüchtg. 38:303-314.

Müller, P. and J. Zeddies. 1988. Economic valuation of varieties and breeding objectives. Plant Breed. 100:59-70.

Obaidi, M., B.E. Johnson, L.D. van Vleck, S.D. Kachman, and O.S. Smith. 1998. Family per se response to selfing and selection in maize based on testcross performance: a simulation study. Crop Sci. 38:367-371.

Rattunde, H.F.W., T. Miedaner, and H.H. Geiger. 1991. Biometrical analysis of alternative plot types for selection in rye. Euphytica 57: 141-150.

Schipprack, W. 1993. Estimation of population parameters and optimization of alternative procedures of recurrent selection in pearl millet (*Pennisetum glaucum* L.). Diss., Univ. Hohenheim, Stuttgart.

Schnell, F.W. 1982. A synoptic study of the methods and categories of plant breeding. Z. Pflanzenzüchtg. 89:1-18.

Schnell, F.W. 1983. Probleme der Elternwahl – Ein Überblick. S. 1-11. *In* Bericht über die Arbeitstagung 1983 der Arbeitsgemeinschaft der Saatzuchtleiter in Gumpenstein, Österreich.

Schnell, F.W. 1996. Über Zuchtplanung und die Entscheidungsspielräume des Pflanzenzüchters. Vortr. Pflanzenzüchtg. 33:227-244.

Schnell, F.W. and H.C. Becker. 1986. Yield and yield stability in a balanced system of widely differing population structures in *Zea mays* L. Plant Breed. 97:30-38.

Sprague, G.F. and W.T. Federer. 1951. A comparison of variance components in yield trials. II. Error, year x variety, location x variety, and variety components. Agr. J. 43:535-541.

Sprague, G.F. and S.A. Eberhart. 1977. Corn breeding. p. 305-362. *In* G.F. Sprague (ed.) Corn and corn improvement. Am. Soc. Agron., Madison, Wisc., USA.

St.Martin, S.K. 1986. Comparison of selection methods for improvement of the population hybrid. Theor. Appl. Genet. 72:682-688.

Stojsin, D. and L.W. Kannenberg. 1994. Genetic changes associated with different methods of recurrent selection in five maize populations. I. Directly selected traits. Crop Sci. 34:1466-1472.

Strahwald, J.F. 1988. Modellrechnungen zur Optimierung der Rekurrenten Selektion bei Gerste. Diss., Univ. Hohenheim, Stuttgart.

Utz, H.F. 1969. Mehrstufenselektion in der Pflanzenzüchtung. Diss., Univ. Hohenheim, Stuttgart.

Utz, H.F. 1982. Der Selektionserfolg in spaltenden Generationen mit experimentellen Untersuchungen und Modellrechnungen beim Weizen. Habilitationsschrift, Univ. Hohenheim, Stuttgart.

Utz, H.F. 1983. Modellstudien zur optimalen Zyklusdauer bei Selbstbefruchtern. Vortr. Pflanzenzüchtg. 3:13-33.

Utz, H.F. 1984. Calculating and maximizing the gain from selection. Vortr. Pflanzenzüchtg. 7:30-40.

Utz, H.F. 1996. PLABSTAT Version 2N. Institut für Pflanzenzüchtung, Saatgutforschung und Populationsgenetik. Universität Hohenheim, Stuttgart.

Vanselow, M. 1990. Effizienz rekurrenter Selektionsverfahren bei Selbstbefruchtern. Experimentelle Ergebnisse bei Hafer und Simulationsstudien. Diss., Univ. Hannover.

van Oeveren, A.J. and P. Stam. 1992. Comparative simulation studies on the effects of selection for quantitative traits in autogamous crops: early selection versus single seed descent. Heredity 69:342-351.

Voylokov, A.V. 1993. Genetic studies of self-fertility in rye (*Secale cereale* L.). I. The identification of genotypes of self-fertile lines for the Sf-alleles of self-incompatibility genes. Theor. Appl. Genet. 87:616-618.

Vermeer, H. Optimising potato breeding. II. A model for optimising single-stage and single-trait selection. Euphytica 53:151-157.

Weber, W.E. 1984. Selection in segregating generations of autogamous species. II. Response to selection in two stages. Euphytica 33:447-454.

Wehmann, F., H.H. Geiger, and A. Loock. 1991. Quantitative-genetic basis of sprouting resistance in rye. Plant Breeding 106:196-203.

Weyhrich, R.A., K.R. Lamkey, and A.R. Hallauer. 1998. Responses to seven methods of recurrent selection in the BS11 maize population. Crop Sci. 38:308-321.

Wilde, P. 1987. Schätzung von Populationsparametern und Untersuchungen zur Effizienz verschiedener Verfahren der Rekurrenten Selektion bei Winterroggen. Diss., Univ. Hohenheim, Stuttgart.

Wilde. P. 1996. Multi-stage selection for combining ability among pollen parent lines in hybrid rye breeding. Vortr. Pflanzenzüchtg. 35:15-25.

Wilde, P. und P. Sepstrup. 1999. Züchtung und Vertrieb von Hybridroggensorten für den europäischen Raum. *In* Bericht über die Arbeitstagung 1999 der Arbeitsgemeinschaft der Saatzuchtleiter in Gumpenstein, Österreich (in press).

Wortmann, H. 1985. Hybridsaatgut-Produktion bei Winterroggen. S. 125-132. *In* Bericht über die Arbeitstagung 1985 der Arbeitsgemeinschaft der Saatzuchtleiter in Gumpenstein, Österreich.

Wricke, G. 1973. Selbstfertile Mutanten beim Roggen und ihre Nutzung in der Züchtung. S. 5-23. *In* Bericht über die Arbeitstagung 1973 der Arbeitsgemeinschaft der Saatzuchtleiter in Gumpenstein, Österreich.

Wricke, G. 1976. Comparison of selection based on yield of half sib progenies and of I_1 lines per se in rye (*Secale cereale* L.). Theor. Appl. Genet. 47:265-269.

Wricke, G. and W.E. Weber. 1986. Quantitative genetics and selection in plant breeding. Walter de Gruyter & Co., N.Y.

7 Appendix

7.1 Flow charts of the breeding schemes investigated

The flow chart of the standard breeding scheme CYC1_11 as well as more information on the breeding schemes presented in the following are given in Section 2.1.

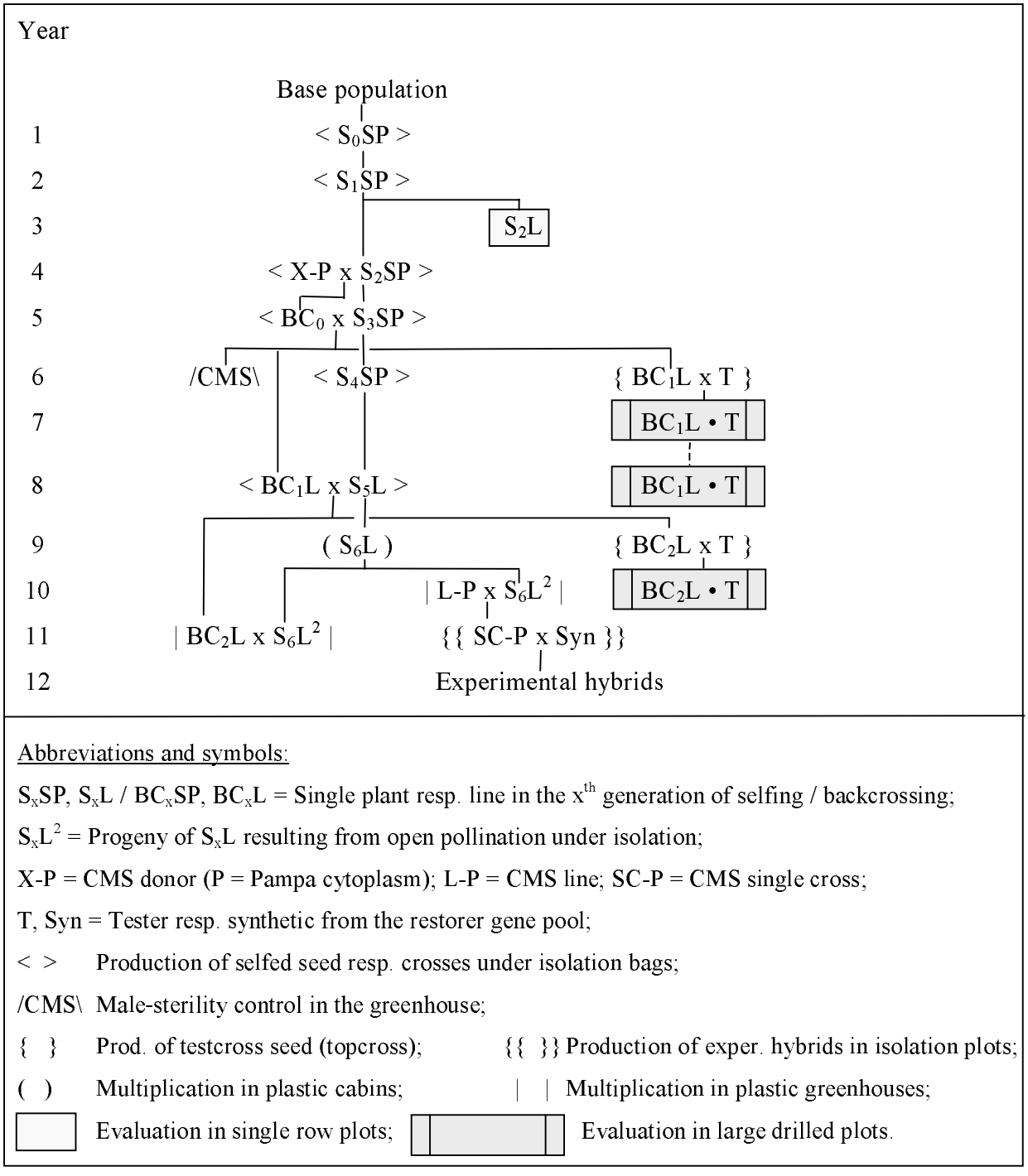

Fig. 7.1. Flow chart of the breeding scheme CYC1_21 employing an additional stage of BC_1L-testcross evaluation compared to the standard scheme (for detailed information and explanation of the name see Section 2.1)

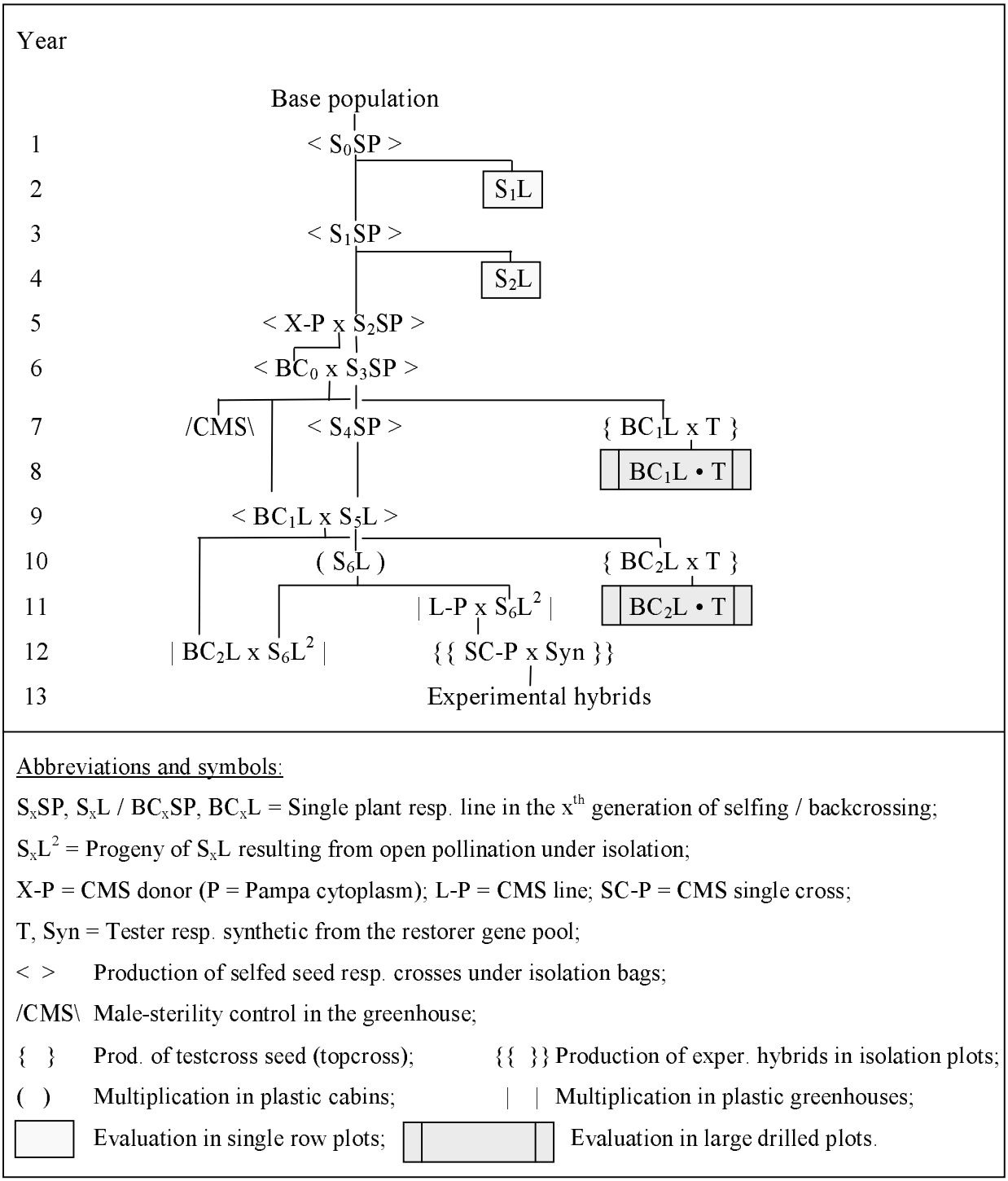

Fig. 7.2. Flow chart of the breeding scheme POP2_11 especially suited for the development of seed-parent lines from broader-based population material (for detailed information and explanation of the name see Section 2.1)

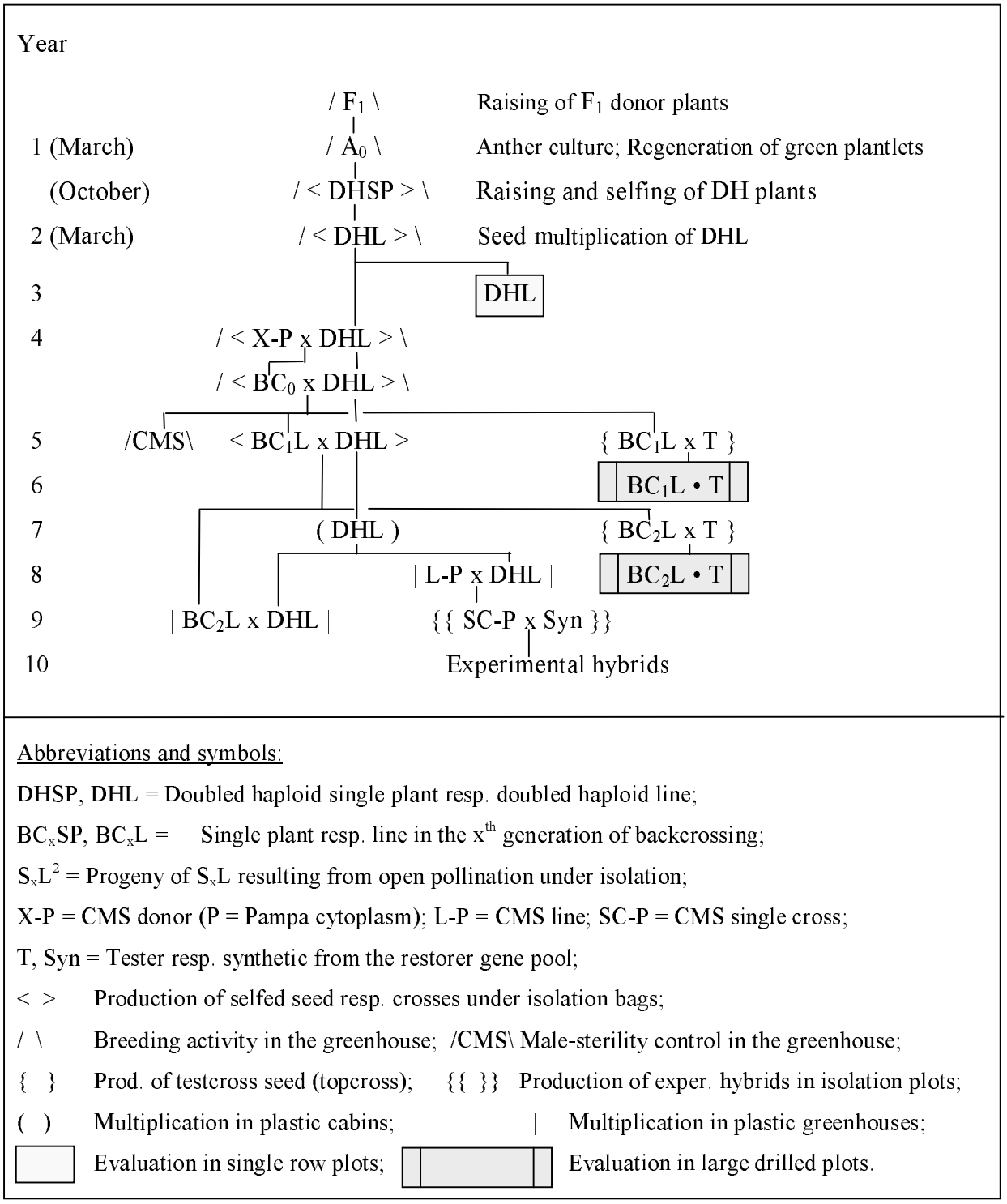

Fig. 7.3. Flow chart of the breeding scheme DHL1_11 employing doubled haploid lines (for detailed information and explanation of the name see Section 2.1)

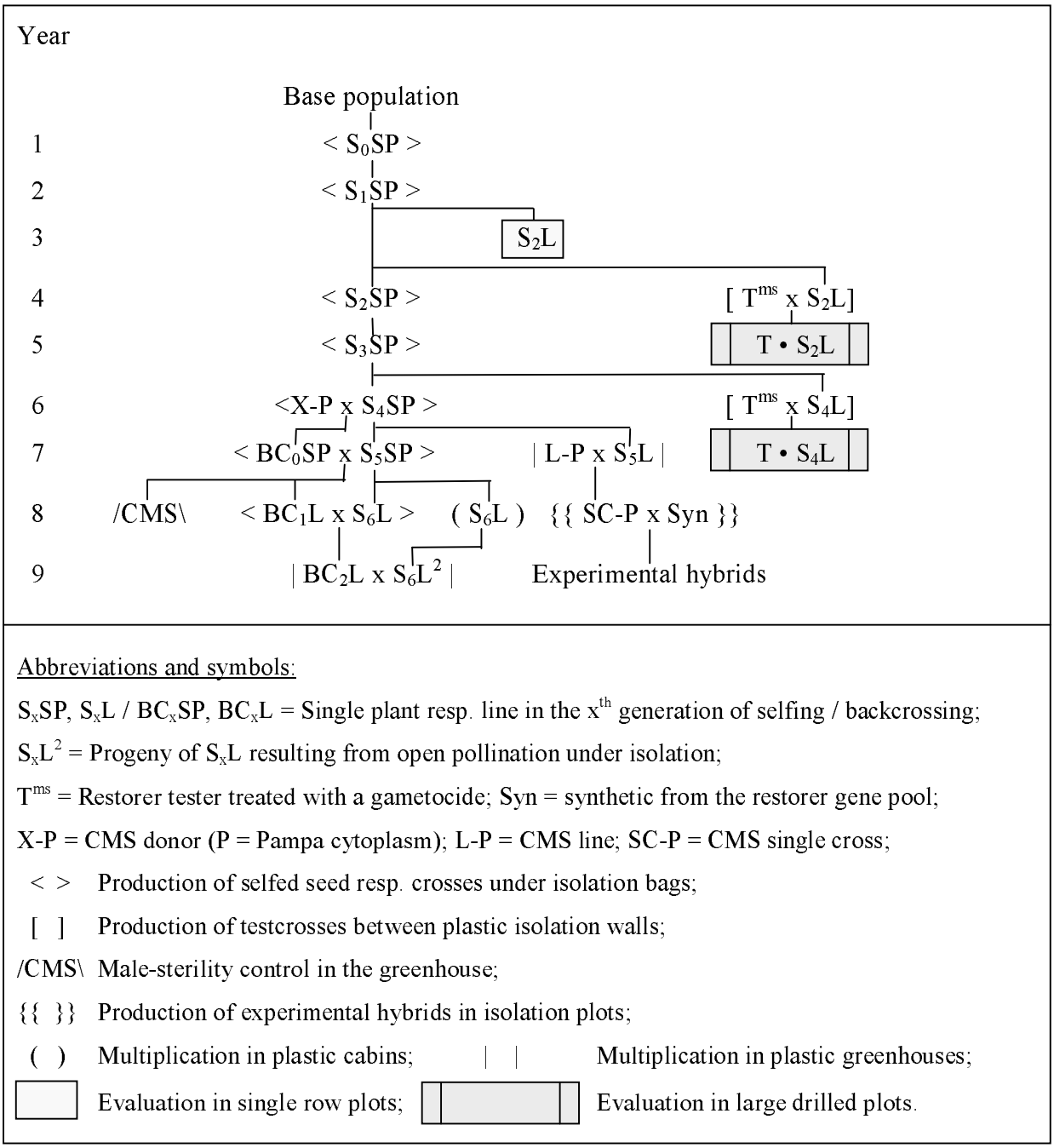

Fig. 7.4. Flow chart of the breeding scheme GAM1_11 employing a gametocide instead of CMS to produce the testcross progenies (for detailed information and explanation of the name see Section 2.1)

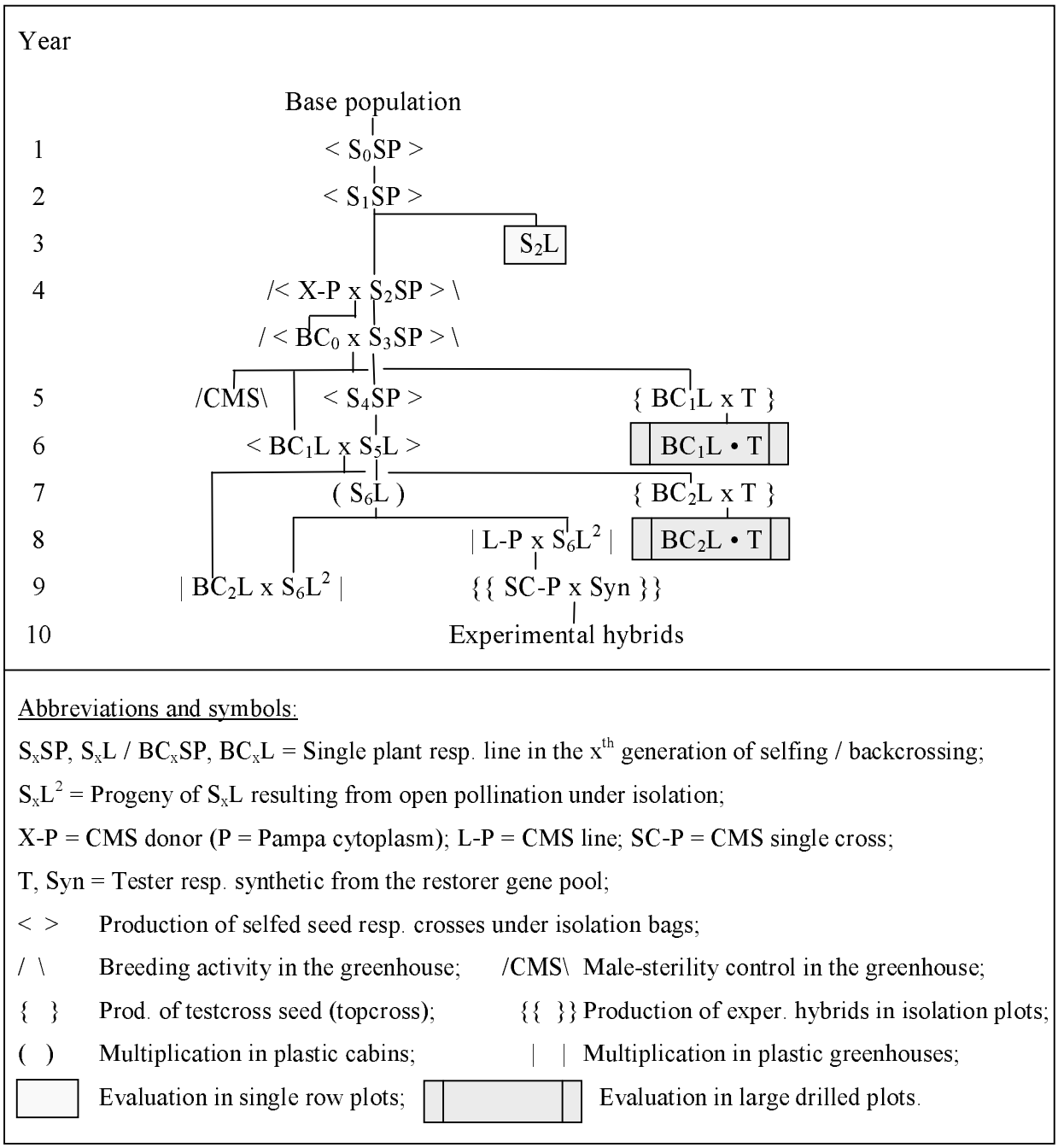

Fig. 7.5. Flow chart of a shortened variant of scheme CYC1_11 in which the BC_0 and BC_1L are developed in one year in the greenhouse (see Section 3.2)

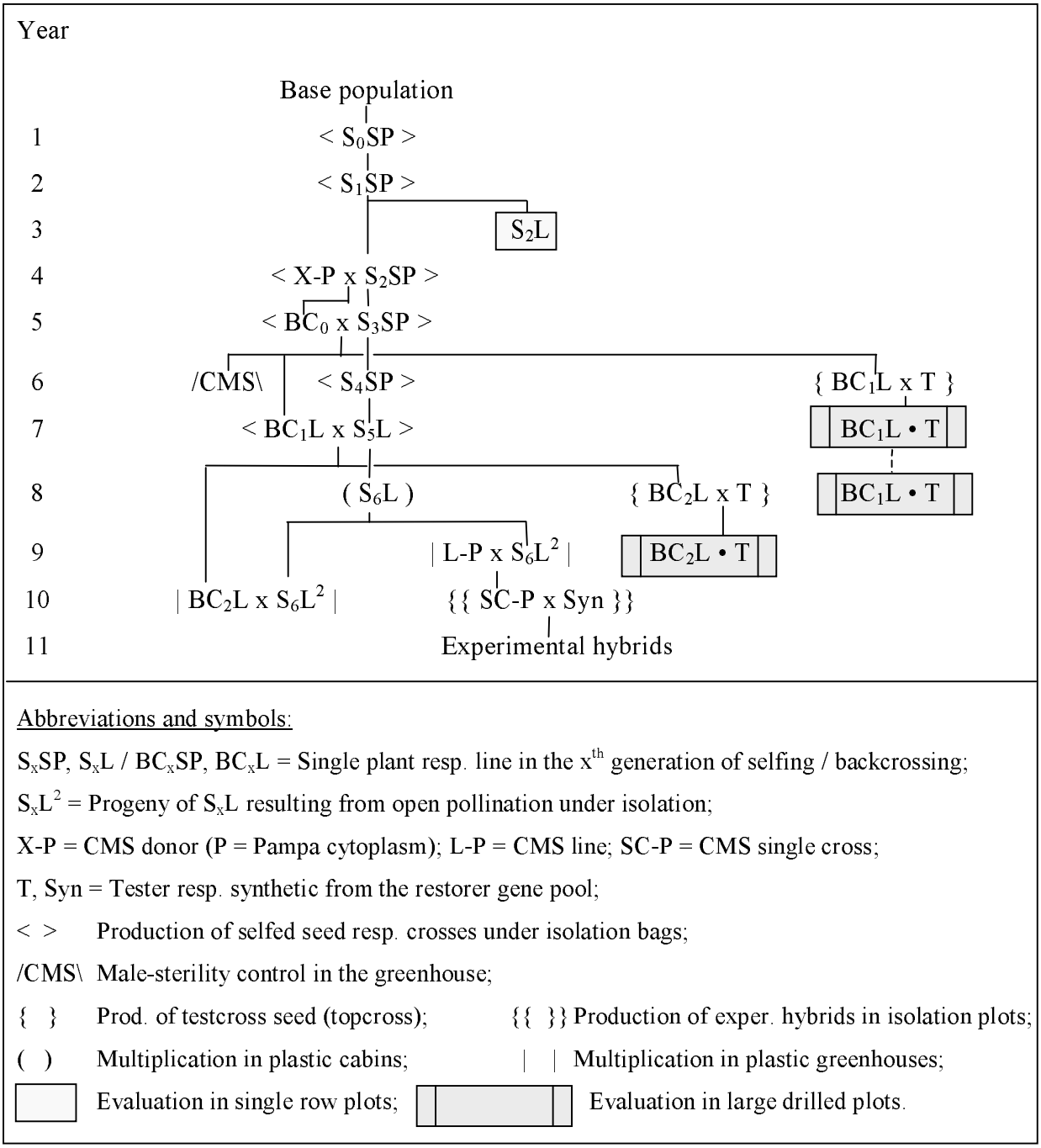

Fig. 7.6. Flow chart of a shortened variant of scheme CYC1_21 in which the BC_2-lines are already developed in parallel to pre-testing the BC_1L-testcrosses (see Section 3.2)

7.2 Computation of the expected gain from multi-stage selection

To calculate the expected gain from multi-stage selection, the formulae given by Cochran (1951) and Utz (1969) were employed in this study. The general formula for the standardized selection gain G_m expected from m selection stages s is:

$$G_m = \frac{1}{\alpha} \sum_{s=1}^{m} \rho_s \, z_s \, I_{ms}$$

where

- α is the total selected fraction with $\alpha = \Pi_s \, \alpha_s$,
  where α_s is the fraction selected at selection stage s,
- ρ_s is the coefficient of correlation between the selection criterion employed at stage s and the gain criterion of selection,
- z_s is the ordinate of the univariate normal distribution in the truncation point k_s of selection stage s, and
- I_{ms} is an incomplete area of the standardized (m-1)-variate normal distribution.

The explicit formulae for the expected standardized gain from single-, two- and three-stage selection thus are:

$$G_1 = \frac{1}{\alpha_1} (\rho_1 \, z_1 \, I_{11}) = \frac{1}{\alpha_1} (\rho_1 \, z_1),$$

$$G_2 = \frac{1}{\alpha_1 \, \alpha_2} (\rho_1 \, z_1 \, I_{21} + \rho_2 \, z_2 \, I_{22})$$

$$G_3 = \frac{1}{\alpha_1 \, \alpha_2 \, \alpha_3} (\rho_1 \, z_1 \, I_{31} + \rho_2 \, z_2 \, I_{32} + \rho_3 \, z_3 \, I_{33}).$$

The respective non-standardized selection gains are easily obtained by multiplying G_m by the standard deviation of the gain criterion.

With index selection the correlation between selection and gain criterion ρ_s is the correlation between the selection index I and the total economic value H. If the traits in the selection index are uncorrelated, ρ_{IH} is calculated as

$$\rho_{IH} = \frac{\Sigma_i \, a_i \, b_i \, \omega_{ty(i)}}{\sigma_I \, \sigma_H} \qquad \text{(Baker, 1986),}$$

where a_i and b_i are the economic and the index weight of trait i, respectively, $\omega_{ty(i)}$ is the covariance between the genotypic effect of the test unit and the target unit in trait i, and σ_I and σ_H are the standard deviations of the selection index resp. of the total economic value.

To calculate the gain in a single trait included in the index, the correlation between selection and gain criterion ρ_s is the correlation between trait i and the selection index I:

$$\rho_{iI} = \frac{b_i \, \omega_{ty(i)}}{\sigma_I \, \sigma_{y(i)}}$$

where $\sigma_{y(i)}$ is the standard deviation of the gain criterion for trait i and the other parameters are defined as described above.

To calculate G_m, first the truncation points k_s (which are needed to calculate the z_s values) have to be determined from the following equations:

$$\alpha_1 = \int_{k_1}^{\infty} PDF_1 \, dt_1,$$

$$\alpha_1 \, \alpha_2 = \int_{k_1}^{\infty} \int_{k_2}^{\infty} PDF_2 \, dt_1 dt_2,$$

$$\alpha_1 \, \alpha_2 \, \alpha_3 = \int_{k_1}^{\infty} \int_{k_2}^{\infty} \int_{k_3}^{\infty} PDF_3 \, dt_1 dt_2 dt_3,$$

where PDF_1, PDF_2, and PDF_3 are the probability density functions of the univariate, bivariate, and trivariate normal distribution, respectively, which are defined as:

$$PDF_1 = (2\pi)^{-1/2} \, e^{-t^2/2}$$

$$PDF_2 = (2\pi)^{-1} \, (1-\rho_{12}^2)^{-1/2} \, e^{\left[-(t_1^2 - 2\rho_{12}t_1t_2 + t_2^2) \, / \, (2(1-\rho_{12}^2))\right]}$$

$$PDF_3 = (2\pi)^{-3/2} \, D^{-1/2} \, e^{\left[-\{(1-\rho_{23}^2)t_1^2 + (1-\rho_{13}^2)t_2^2 + (1-\rho_{12}^2)t_3^2 + 2(\rho_{13}\rho_{23} - \rho_{12})t_1t_2 + 2(\rho_{12}\rho_{23} - \rho_{13})t_1t_3 + 2(\rho_{12}\rho_{13} - \rho_{23})t_2t_3\} \, / \, (2D)\right]}$$

$$\text{with } D = 1 + 2\rho_{12}\rho_{13}\rho_{23} - \rho_{12}^2 - \rho_{13}^2 - \rho_{23}^2.$$

In the foregoing equations, $\rho_{ss'}$ denotes the coefficient of correlation among the selection criteria used at selection stages s and s': $\rho_{ss'} = \omega_{tt'} / (\sigma_{xs}\sigma_{xs'})$, where $\omega_{tt'}$ is the covariance between the genotypic effects of the test units at selection stages s and s' and σ_{xs} resp. $\sigma_{xs'}$ are the phenotypic standard deviations of the test units at selection stages s resp. s'.

For the present study, the uni-, bi-, and trivariate normal integrals needed were determined numerically employing Simpson's rule and the above PDF. Integration limits of ± 6 were chosen for the uni- and bivariate normal integral for this purpose. For the trivariate normal

integral, the limits were fixed at ± 4. This doesn't affect the accuracy of the results since the ordinate at this point is practically zero (Utz, 1969). The bi- and trivariate normal integrals were determined for a range of correlation coefficients $\rho_{ss'} = 0.1$ to 0.95. For each type of integral the results of the numerical integration were stored in a file. From these results, any truncation point k_s belonging to a given integral α can now be found by interpolation and *vice versa* (see below). Interpolation is carried out using Lagrange polynoms. The accuracy of the results was checked using tables of Gupta (1963). The normal integrals and truncation points obtained by interpolation were found to be accurate to four to five relevant decimal places in case of two-stage selection and to three decimal places in case of three-stage selection.

Calculating, for example, the gain from three-stage selection requires the input parameters α_1, α_2, α_3, ρ_1, ρ_2, ρ_3, and ρ_{12}, ρ_{13}, ρ_{23}. As a first calculation step, the truncation points k_s are determined one by one by interpolation from the stored integral values. First, the value k_1 belonging to α_1 is found from the univariate distribution. Then k_2 can be determined for the given integral $\alpha = \alpha_1\alpha_2$, the truncation point k_1, and the between-stages correlation coefficient ρ_{12}. Finally, k_3 is derived analoguously from the trivariate distribution with $\alpha = \alpha_1\alpha_2\alpha_3$, the truncation points k_1 and k_2, and the correlation coefficients ρ_{12}, ρ_{13}, and ρ_{23}.

After the truncation points have been found, the respective ordinates are calculated as:

$$z_s = (2\pi)^{-1/2}\, e^{-k_s^2/2} .$$

The last parameters needed are the incomplete areas of the standardized (m-1)-variate normal distribution. They are defined as:

$$I_{11} = 1$$

$$I_{21} = \int_{A_{12}}^{\infty} PDF_1 \qquad I_{22} = \int_{A_{21}}^{\infty} PDF_1$$

$$I_{3q} = \int_{A_{qi}}^{\infty}\int_{A_{qj}}^{\infty} PDF_2\,(\rho_{ij\_q}) \qquad \text{for } q = 1, 2, 3 \text{ and } i < j \neq q$$

$$\text{with } \rho_{ij\_q} = (\rho_{ij} - \rho_{iq}\rho_{jq}) \,/\, \sqrt{(1-\rho_{iq}^2)\,(1-\rho_{jq}^2)} .$$

The I_{ij} are again determined from the stored integral values by interpolation. The lower integration limits, A_{ij}, needed for this purpose are obtained as:

$$A_{ij} = (k_j - \rho_{ij}k_i) \,/\, \sqrt{(1-\rho_{ij}^2)} \qquad \text{with } \rho_{ij} = \rho_{ji}.$$

With two-stage selection the integrals I_{21} resp. I_{22} depend only on the lower integration limits A_{12} resp. A_{21}. In case of three-stage selection, however, the correlation coefficients ρ_{ij_q} (see above) are additionally required to determine the bivariate normal integrals I_{31}, I_{32}, and I_{33}.

7.3 Derivation of the coefficients of coancestry for BC_1- and BC_2-lines

The coefficient of coancestry, *f*, between any two individuals is the probability that two gametes taken at random, one from each individual, carry alleles that are identical by descent (Falconer and Mackay, 1996). It is identical with the inbreeding coefficient of their progeny if the two individuals were mated. The coefficient of coancestry can be derived from the pedigree of the individuals of interest. For a general pedigree, the coancestry among two individuals P and Q is the mean of the four coancestries among their parents A and B resp. C and D: $f_{PQ} = ¼ [f_{AC} + f_{AD} + f_{BC} + f_{BD}]$. A special case is the coancestry of an individual A with itself, $f_{AA} = ½ (1 + F_A)$, where F_A is the inbreeding coefficient of individual A.

To calculate the variance among BC_1-testcross progenies, one has to derive the coefficient of coancestry among two random individuals of the same BC_1-line. Each BC_1-line is produced by crossing a BC_0-single plant with an S_3-single plant and consists of individuals $BC_{1(1)}$ to $BC_{1(n)}$. The coefficient of coancestry among two of these individuals, e.g. BC_1 and $BC_{1'}$, is:

$$f(BC_1, BC_{1'}) = ¼ [f_{BC_0\ BC_0} + f_{BC_0\ S_3} + f_{BC_0\ S_3} + f_{S_3\ S_3}],$$

where

$f_{BC_0\ BC_0} = ½ (1 + F_{BC_0}) = 0.5,$ (since $F_{BC_0} = 0$),

$f_{BC_0\ S_3} = F_{BC_1} = 0.4375,$

$f_{S_3\ S_3} = ½ (1 + F_{S_3}) = 0.9375,$

so that $f(BC_1, BC_{1'}) = 0.5781$.

Analogously, the coefficient of coancestry among two individuals of a BC_2-line is derived as

$$f(BC_2, BC_{2'}) = ¼ [f_{BC_1\ BC_1} + f_{BC_1\ S_5} + f_{BC_1\ S_5} + f_{S_5\ S_5}],$$

where

$f_{BC_1\ BC_1} = ½ (1 + F_{BC_1}) = 0.7188,$ (since $F_{BC_1} = 0.4375$),

$f_{BC_1\ S_5} = F_{BC_2} = 0.6875,$

$f_{S_5\ S_5} = ½ (1 + F_{S_5}) = 0.9844,$

so that $f(BC_2, BC_{2'}) = 0.7695$.

If DHL are employed to produce the BC_1- and BC_2-lines instead of S_3- resp. S_5-lines, the coefficients of coancestry are obtained as:

$$f(BC_{1\_DH}, BC_{1\_DH}') = ¼ [f_{BC_{0\_DH}\ BC_{0\_DH}} + f_{BC_{0\_DH}\ DH} + f_{BC_{0\_DH}\ DH} + f_{DH\ DH}] = 0.625, \quad \text{and}$$

$$f(BC_{2\_DH}, BC_{2\_DH}') = ¼ [f_{BC_{1\_DH}\ BC_{1\_DH}} + f_{BC_{1\_DH}\ DH} + f_{BC_{1\_DH}\ DH} + f_{DH\ DH}] = 0.8125.$$

7.4 Short description of the computer programs

To determine the optimum allocation of the alternative breding schemes investigated in the present study, computer programs were developed using the C++ programming language. Each breeding scheme studied is represented by a specific optimization program of similar modular structure. A strongly simplified graphical representation of the general structure and function of the programs is given in Figure 7.7. It is explained in more detail in the following.

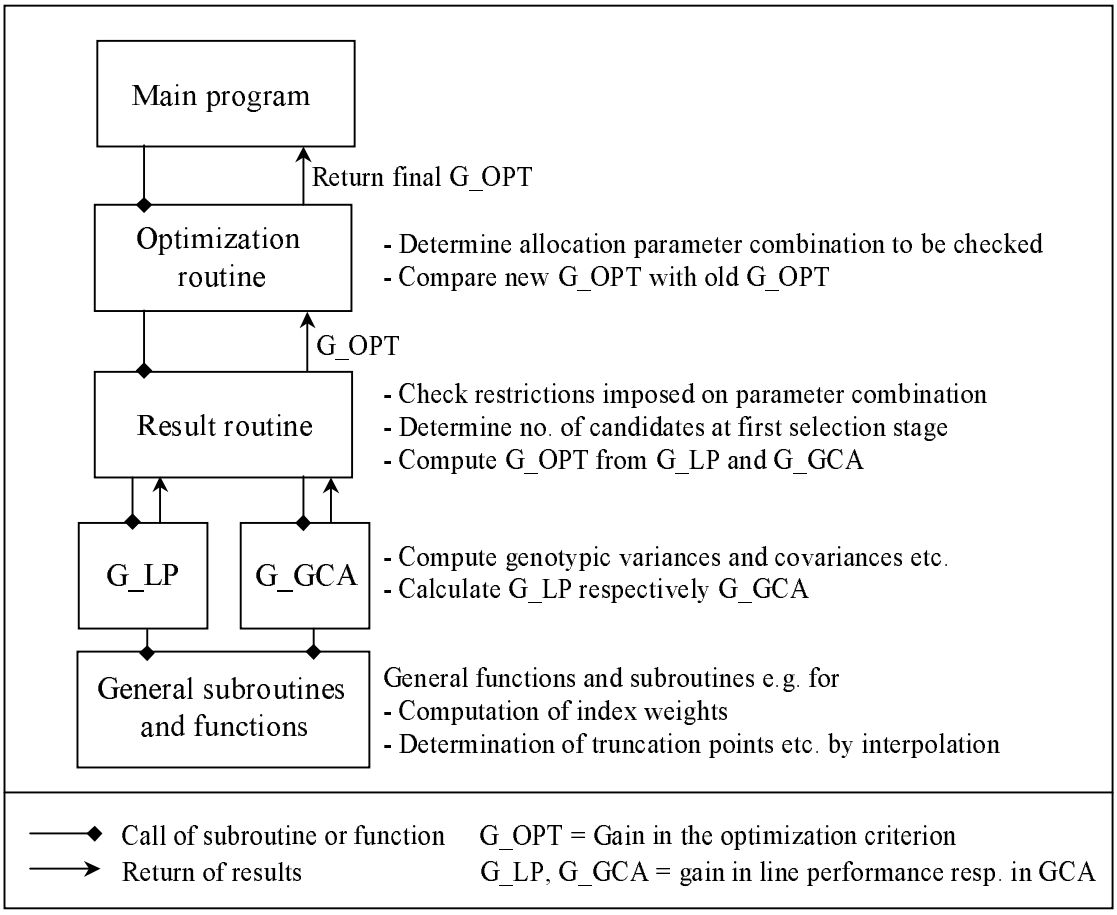

Fig. 7.7. General structure of the optimization programs developed for the present study

When the optimization program is started, first all input parameters required are read from a text-file. This file contains all the quantitative-genetic and economic parameters, the relevant restrictions, and the minimum and maximum values assigned to the allocation parameters to be optimized (see Section 2.4). All parameter values in the file can easily be altered by the

user. After the input parameters are read, the main program calls the optimization routine (Fig. 7.7). The optimization routine employs an n-dimensional grid search approach to find that combination of the n allocation parameters that gives the highest expected selection gain (see Section 2.4). First, the actual set of allocation parameters to be checked is determined in the optimization routine (see Section 2.4). Afterwards, the scheme-specific result routine is called which is employed to calculate the gain in the optimization criterion for a given set of allocation parameters. In the result routine, first the restrictions imposed on the combinations of the allocation parameters are checked (e.g. that the number of candidates doesn't increase from one selection stage to the next). To guarantee that only combinations making full use of the budget are investigated (see Section 2.4), the number of candidates at the very first stage of selection in the breeding scheme is not determined by the optimization routine. Instead, it is obtained from a cost function that describes the technical process of the particular breeding scheme precisely. In this function, the costs caused by advancing and evaluating the presently assumed numbers of candidates, except those at the first selection stage, with the presently assumed numbers of testers, locations, and replicates are calculated and subtracted from the total budget. The number of candidates at the first selection stage is then obtained by dividing the remaining budget by the costs related to the production and evaluation of each of these candidates. Now the result function calls the subroutines to compute the direct selection gains in line performance (G_LP) and in GCA (G_GCA). These subroutines are specific with respect to the number of selection stages, the types of test units employed at each evaluation stage, and – for computing the gain in GCA – with respect to the number of preceding stages of selection on line performance (for which a correction of the combining ability variances is carried out; see Section 2.2.2). To allow a bigger flexibility in combination, these subroutines were implemented as separate modules and not as complete scheme-specific subroutines. Computation of the selection gain in these modules involves (i) calculation of the genotypic and phenotypic variances in the selection criterion, the variance in the gain criterion, and the covariances between selection and gain criterion and between test units of different selection stages, and (ii) the determination of the truncation points and the incomplete areas of the multivariate normal distributions from the stored integral values by interpolation (see Section 7.2). For many of these computations (e.g. for the interpolation), non-specific functions were implemented that are used by all the gain modules. The gain modules return the selection gains in line performance and in GCA to the result routine, which finally computes the gain in the optimization criterion and returns this result to the optimization routine. The result is

compared with the last optimization result. The next round of optimization is started. This procedure is repeated until the optimum allocation of resources is found.

When the optimum allocation of resources has been determined, the indirect and total gains in line performance and GCA for the indices as well as for the individual traits are calculated. Another scheme-specific subroutine computes the proportions of the budget spent on the individual operations belonging to the breeding procedure (see Section 3.1). Finally, all the results are stored and can be printed in an output file.

7.5 Relative gain of the alternative breeding schemes under various assumptions

Table 7.1. Selection gain in the valuation criterion (G_VAL) of the alternative breeding schemes relative to that of the respective optimum variant of the standard scheme under various assumptions regarding the quantitative-genetic and economic parameters underlying the model calculations (for descriptions of the variants see Sections 2.3 (STD) and 3.3)

Variant	G_VAL for	Relative G_VAL [%]			
	CYC1_11	CYC1_21	POP2_11	DHL1_11	GAM1_11
STD	0.156	94.2	86.5	107.7	131.4
G_Low	0.110	93.6	86.4	107.3	130.9
G_High	0.222	93.7	86.5	106.8	130.6
D_Low	0.175	94.3	86.3	106.9	132.6
D_High	0.120	92.5	86.7	107.5	128.3
E_Low	0.157	93.6	86.6	106.4	130.6
E_High	0.155	93.5	86.5	107.7	131.6
GxE_Low	0.166	93.4	86.1	106.6	131.3
GxE_High	0.143	94.4	86.7	107.7	130.8
REV_{GY} = 3	0.129	93.8	87.6	106.2	129.5
REV_{GY} = 12	0.208	94.2	85.6	107.2	132.7
W_{LP}:W_{GCA}					
= 0.4 : 0.6	0.163	92.6	87.1	109.2	126.4
= 0.1 : 0.9	0.159	95.0	85.5	108.2	137.7
€ 100,000	0.141	93.6	86.5	105.7	127.0
€ 200,000	0.156	94.2	86.5	107.7	131.4
€ 300,000	0.164	93.9	86.6	107.9	132.9
€ 400,000	0.170	93.8	86.5	108.2	132.9

Danksagung

Besonders herzlich danken möchte ich Herrn Prof. Dr. H.H. Geiger - nicht nur für die Überlassung des Themas, sondern vor allem für die zahlreichen anregenden Diskussionen und die hervorragende Betreuung während dieser Arbeit.

Mein herzlicher Dank gebührt Herrn PD Dr. Th. Miedaner für seine ständige Diskussions- und Hilfsbereitschaft, zahlreiche wertvolle Anregungen und nicht zuletzt die 'moralische' Unterstützung in kritischen Phasen der Arbeit.

Die praktischen Roggenzüchter Herr Dr. E. Knopf, Herr Dr. P. Wilde, Herr Dr. H. Wortmann und Herr Dr. F.J. Fromme haben mir nicht nur umfangreiches Datenmaterial zur Verfügung gestellt, sondern vor allem durch die Vorstellung und Erläuterung ihrer Zuchtprogramme, viele ausführliche Gespräche und zahlreiche hilfreiche Anregungen ganz maßgeblich zum Gelingen dieser Arbeit beigetragen. Dafür möchte ich mich ganz herzlich bedanken.

Dem Bundessortenamt und besonders Herrn Dr. Rentel danke ich für die Überlassung von Ergebnissen der Wertprüfungen für Winterroggen.

Aufgrund seiner eigenen Erfahrungen mit dieser Thematik war mir Herr Dr. D.C. Borchardt besonders am Anfang des Projektes eine große Unterstützung.

Viele Mitarbeiter am Institut für Pflanzenzüchtung, Saatgutforschung und Populationsgenetik haben auf die eine oder andere Weise zum Fortgang und Gelingen dieser Arbeit beigetragen. Besonders erwähnen möchte ich an dieser Stelle Herrn Dr. H.F. Utz, Herrn Dr. Th. Presterl, Frau G. Kraft, Frau S. Egelhaaf und Herrn Dr. F.M. Gumpert. Mein ganz besonderer Dank gilt meinem Mann Kai, der mir während der gesamten Arbeit eine große Stütze war.

Bei Herrn Prof. Dr. W.E. Weber und Herrn PD Dr. H.-P. Piepho möchte ich mich für das Interesse an meiner Arbeit bedanken.

Das dieser Dissertation zu Grunde liegende Forschungsvorhaben wurde vom Bundesministerium für Ernährung, Landwirtschaft und Forsten (BML) und der Gemeinschaft zur Förderung der privaten deutschen Pflanzenzüchtung e.V. (GFP) gefördert (Projekt-Nr. G 81/98 HS). Beiden Institutionen sei für die finanzielle Unterstützung gedankt.

Lebenslauf

Name:	Alexandra-Maria Tomerius	
Geboren:	am 20. Juli 1970 in Wolfenbüttel als Tochter des Gynäkologen Dr. med. Reinhard Tomerius und seiner Ehefrau Edelgard Tomerius geb. Brachmann	
Familienstand:	verheiratet mit Kai Tomerius geb. Gogl seit August 1999	
Schulausbildung:	1977-1981	Grundschule Wallstraße, Wolfenbüttel
	1981-1983	Orientierungsstufe Wallstraße, Wolfenbüttel
	1983-1987	Gymnasium im Schloß, Wolfenbüttel
	1987-1990	Otto-Hahn-Gymnasium, Göttingen
	Mai 1990	Zeugnis der Allgemeinen Hochschulreife
Studium:	WS 1990/91 Agrarwissenschaften an der Universität Gießen SS 1991 - SS 1996 Allgemeine Agrarwissenschaften an der Universität Hohenheim, Fachrichtung Pflanzenproduktion, Diplomabschluß im Juli 1996	
Landw. Praxis:	Februar 1991 - April 1991 Landw. Betrieb H. Alber, Filderstadt Mai 1993 – September 1993 Landessaatzuchtanstalt Hohenheim	
Berufl. Tätigkeit:	August 1996 - Juli 1998 wissenschaftliche Mitarbeiterin der CE Pflanzenzucht Dr. h.c. Carsten, Inh. Erhardt Eger KG, Bad Schwartau	
	November 1998 – Oktober 2000 wissenschaftliche Mitarbeiterin am Institut für Pflanzenzüchtung, Saatgutforschung und Populationsgenetik der Universität Hohenheim	
	Januar bis voraussichtlich Juni 2001 wissenschaftliche Mitarbeiterin der Lochow-Petkus GmbH, Bergen Kr. Celle	