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Towards understanding the genetics of tolerance to low soil phosphorus conditions in West African pearl millet

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Towards understanding the genetics of tolerance to low soil phosphorus conditions in West African pearl millet

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[1] Gemenet D.C., Hash C.T., Sy O., Zangre, R.G., Sanogo, M.D., Leiser W.L., Parzies H.K. and Haussmann B.I.G. (2014). Pearl millet inbred and testcross performance under low phosphorus in West Africa. Crop Sci. 54:2574–2585.

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List of Abbreviations

+P	with phosphorus fertilizer
AM	arbuscular mycorrhiza
ATP	adenosine triphosphate
CO_2	carbon dioxide
DArT	diversity array technology
DNA	deoxyribonucleic acid
FAO	food and agriculture organization of the United Nations
FD	flowering delay
FLO	days to flowering
G x E	genotype-by-environment
G x P	genotype-by-phosphorus interaction
GBS	genotyping-by-sequencing
GGE	genotype and genotype-by-environment biplot
GY	grain yield
HI	harvest index
HP	high phosphorus
LP	low phosphorus
N	nitrogen
P	phosphorus
-P	without phosphorus fertilizer
PE	phosphorus efficiency
QTL(s)	quantitative trait locus (loci)
r_g	genetic correlation
r_p	phenotypic correlation
SNP	single nucleotide polymorphism
SSA	Sub-Saharan Africa
SSR	simple sequence repeat
WA	West Africa

General Introduction

Sub-Saharan Africa (SSA) faces cereal deficits of about nine million tons annually and this is projected to triple to about 35 million tons annually by 2025, a level which SSA Africa is not likely to be able to finance (Cooper et al. 2008). As a result, about 223 million people are undernourished in SSA with about 11 million people being food insecure in the Sahel region of West Africa (WA; FAO et al. 2013). SSA is the lowest consumer of inorganic fertilizers with WA, Central Africa and East Africa recording less than 12 kg ha^{-1} each (FAO 2014). Global food security is threatened by the looming depletion of rock phosphate reserves (Cordell et al. 2009). This situation has the ability of causing fertilizer price escalation, a burden that cannot be managed by resource poor farmers in SSA. Many tropical soils including the acid savannas like those in the Sahel region of WA have low plant available phosphorus (P) and high P fixation potential coupled with other mineral toxicities and/or deficiencies and this is a major constraint on pearl millet production within the region (Hash et al. 2002; Kochian 2012). Breeding for increased grain yield under low-P conditions in pearl millet will not only contribute towards the food security within the WA Sahel in the short term but also in the long term by contributing towards the efficient use of a scarce resource.

Global food security by the year 2050

Presently, 827 million people, about 12% of the global population are undernourished (FAO et al. 2013). It is estimated that the world population will be about nine billion people by 2050 (Lutz and Samir 2010). Given the projected improved diets, increased consumption and increased incomes, the population increase will call for an increase of between 70-100% in food production (UNFPA 2010). According to Bruinsma (2009), cereal yields will need to be increased by about 49% whereas increased demand for bio-fuels will need an extra 9% to 19% increase in cereals (Fischer 2009). These will require annual harvests to increase by 1.16% to 1.31% yr^{-1} (Hall and Richards 2013). The demand for increased food production can be achieved by increasing productivity on the existing farm land, expanding crop area or by both approaches (Wart et al. 2013). The latter option is limited by several factors including scarcity of currently unexploited agriculturally productive soils, release of CO_2 from soil organic matter following conversion of grasslands and/or forests to crop lands, the need to conserve important and/or fragile ecosystems and the conversion of agricultural land to other non-agricultural uses such as urban development (Hall and Richards 2013). Therefore this increased demand on food will need to be provided mainly on the same agricultural land area. The applicability of this depends on the yield potential of the crop in question i.e. the maximum attainable yield per unit land area that can be achieved by a given crop in an environment where it is adapted with effectively controlled abiotic and biotic stresses (Evans 1993). There is evidence that yield of some of the world's main cereals have reached a plateau in certain regions of the globe, e.g. rice in Japan and China, maize in China, Italy and France, wheat in northern Europe and India (Brisson et al. 2010; Cassmann et al. 2010, Wart et al. 2013). Yield potential for most crops has not been attained in Africa especially in SSA due to several constraints such as rainfall variability, production uncertainty, climate change, lack of infrastructure, unavailability of inputs, lack of effective markets, lack of technical know-how, among others, thereby leaving a window for increasing yields (Cooper et al. 2008). This 'Africa option' has been explored in recent years by multinational corporations but it has been marred by ethical issues and it is now agreed that the key to fighting hunger and poverty lies in the equitable rights to access land and other natural resources by the poor and vulnerable smallholder farmers (FAO 2012).

Abiotic stresses and food security

Stress refers to external conditions that adversely affect growth, development or productivity (Lutts and Kinet 1998; Gasper et al. 2002). Abiotic stresses have become a major threat to global food security due to constant changes in climates as well as environmental deterioration due to human activity (Yang et al. 2013; Huang et al. 2013; Rao et al. 2013; Araujo et al. 2014). They are known to cause yield losses of up to 50% in major crop plants (Wang et al. 2003). Development of abiotic stress tolerance crops is therefore a major step towards increasing yields and ensuring global food security (Bansal et al. 2014; Henry 2014). Breeding for tolerance to abiotic stresses is mainly limited by the fact that stresses occur in combination under field conditions (Mittler 2006) therefore making crop performance under stress a result of many genes having numerous interactions with the environment and cultural practices (Atikinson and Urwin 2012; Araujo et al. 2014). Plant adaptation to a given stress condition thus requires a specific response that is tailored to the precise environmental conditions the plant finds itself in (Mittler 2006). Increasing grain yields under abiotic stress in crop plants has been successfully achieved in the past century by conventional plant breeding with little or no knowledge of the genetic factors governing the genetic variability exploited by breeders (Blum 1988; Borlaug 2007). Currently, various genomic approaches are available that can be applied in research to better understand plants' responses to abiotic stress including quantitative trait loci (QTL) mapping, genome wide association mapping, genomic selection and transcriptome profiling (Garg et al. 2014). Low soil P is one such abiotic stress limiting crop production worldwide due to its low availability and inaccessibility in the soil (Holford 1997; Vance et al. 2003; Wang et al. 2010).

Phosphorus and global food security

Global food security in the future will depend on the availability of P since it has no substitute in crop growth and cannot be manufactured (Cordell and White 2013). Phosphate rock from which most of the P used in agricultural systems is obtained has been shown to be a scarce and non-renewable resource which needs to be used efficiently in order to either maintain the current agricultural productivity or increase it to be able to feed the rising population (Cordell et al. 2009; Veneklaas et al. 2012). As a constituent of nucleic acids, phospholipids and adenosine triphosphate (ATP) molecules, P is an important macronutrient for all living organisms (King et al. 2013; Hufnagel et al. 2014). Depending on factors such as demand rate, P concentration and economic viability, several sources have estimated that phosphate rock reserves will be exhausted by between 40-400 years (Vaccari 2009; Cooper et al. 2011; Dawson and Hilton 2011; Jasinski 2011; Cordell and White 2013; Obersteiner et al. 2013). Two thirds of the cultivated soils in the world are affected by P deficiency (Batjes 1997) which is more critical in highly weathered soils of the tropics and subtropics, as well as calcareous/alkaline soils of Mediterranean basin (Hinsinger 2001). Sub-Saharan Africa is currently the least consumer of P fertilizer (<5 kg P ha^{-1}, Obersteiner et al. 2013). With the looming geopolitics and the estimated P peak (where P demand will exceed supply) likely to occur before 2040 (Cordell and White 2013), it is unlikely that smallholder pearl millet farmers in WA will be able to afford the P price.

Pearl millet as a food security crop

Pearl millet, [*Pennisetum glaucum* (L.) R. Br. syn. *Cenchrus americanus* (L.) Morrone], 2n = 2x = 14, is a member of the grass family Poaceae with a DNA content of 2C = 4.71pg. The crop is highly out-crossing and has a lot of wild relatives (2n = 10, 14, 16 and 18; Martel et al. 1997). It is the hardiest of the C4 plants growing in the driest and hottest regions of Africa and the India subcontinent and it is therefore an important crop for food security in these regions (Mariac et al. 2006; Supriya et al. 2011). Pearl millet is said to have been domesticated in north-eastern Mali about 4500 years ago (Manning et al. 2011) and this makes WA a diversity hot spot for pearl millet. Currently it is estimated to be produced on more than 10 million ha in Asia and about 16 million ha in Africa (Rai et al. 2009). Being a staple cereal in these regions, pearl millet contributes to food security by providing both calories and essential micronutrients. With about two billion people in the world being micronutrient malnourished, and more so in developing countries like WA (Birner et al. 2007; Muthayya et al. 2013), pearl millet has been shown to have higher iron and zinc contents than most cereals (Cercamondi et al. 2013; Kodkany et al. 2013; Bachir et al. 2014a, 2014b: Pucher et al. 2014). Compared to its contribution to humanity, pearl millet has received less research attention and it is still considered an ‘orphan’ crop (Supriya et al. 2011). For instance, people who rely on this crop did not benefit from the ‘biotechnology revolution’ until 2005 when the first marker-assisted selection product was obtained (Hash et al. 2006). Nevertheless, progress has been made to correct this situation and a draft pearl millet genome sequence is expected to be published soon.

Pearl millet production in Sahelian West Africa

Open-pollinated pearl millet varieties are the predominant cultivars grown in WA (Velu et al. 2011) since the seed can be easily recycled by farmers. Smallholder farmers in the WA region have been said to still predominantly grow landraces (Busso et al. 2000; Dingkuhn et al. 2006) compared to improved open-pollinated varieties. This has been attributed to seed supply constraints such as low supply of breeder seed, poor seed-demand estimates, poor distribution systems, low seed quality and demand constraints that mainly have to do with farmer preferences which may differ from those provided for by the improved varieties (Ndjeunga et al. 1997, 2002). Landraces are also more adapted to the highly variable environmental conditions within the region and smallholder farmers in WA have been said to grow several varieties at the same time (Haussmann et al. 2012). This increases intra-varietal genetic variance which acts as a population buffering strategy to avert risks associated with the harsh growing conditions of unpredictable drought, low soil water-holding capacity, and high temperatures (Brück et al. 2003; Haussmann et al. 2007, 2012).

Pearl millet grain yields have remained low within the WA region (<500 kg ha^{-1}) due to the interaction between low-soil fertility, drought and poor management systems (Buerkert et al. 2002; Gandah et al. 2003; de Rouw 2004) with P having been shown to be the most limiting soil macronutrient to pearl millet productivity in the Sahel region (Bationo and Mokwunye 1991). Most of the smallholder farmers’ fields have plant-available P values of less than the critical value recommended for the region (7 mg P kg^{-1} soil; Manu et al. 1991; Doumbia et al. 2003). This is attributed to the highly weathered and acidic soils possibly with a high P retention as well as with the capacity to fix between 70-90% of applied fertilizers (Holford 1997; Kochian 2012). Poor rural infrastructure causes inaccessibility of fertilizers; the increasing prices also make fertilizer use out of reach for most smallholder farmers (Obersteiner et al. 2013). Therefore intensive use of fertilizers to increase pearl millet grain yields in this region is unlikely to be a feasible option. Breeding for low-P tolerance is therefore the main environmental friendly and economically feasible strategy for improving crop productivity under low-P soils for smallholder farmers in WA conditions. This is the first study to specifically address breeding issues for low-P soil conditions in WA pearl millet production systems.

Breeding strategy for pearl millet targeting low-P environments in WA

The success of a breeding program depends on significant levels of genetic variability for the target trait in the original population and an efficient selection method for the fixation of desirable genetic combinations. It has been shown that plants are exposed to combinations of different stresses under field conditions (Mittler 2006). For instance, the holistic effect of low soil P stress on pearl millet grain yield in WA is an interaction among many factors including drought, the soil physical and chemical environment as well as biological interactions (Hash et al. 2002). This makes low-P tolerance a quantitative trait under the control of the collective effects of many quantitative trait loci (QTLs), the interaction between these loci (epistasis), the environment and the interaction between the QTLs and the environment (Semagn et al. 2010). This therefore brings in the issue of genotypic adaptation (Finlay and Wilkinson 1963; Ceccarelli 1994) in two dimensions: in terms of locations and years (spatial and temporal terms) within the target region and in terms of P-levels. For locations and years, there is need to properly define the amount and type of genotype-by-environment (G x E) interaction within the target region so as to decide on whether to breed for wide adaptation (genotypes that perform well in a considerable range of environments) or for specific adaptation (genotypes that perform well in predictable, closely defined ecological conditions; Finlay and Wilkinson 1963; Yan and Hunt 2001). In terms of P-level, there is need to define the amount and pattern of genotype-by-P-level interaction so as to decide on whether to select genotypes targeting low-P environments under low-P conditions (direct selection) or to select under optimal-P conditions and rely on a correlated selection response for performance under low-P conditions (indirect selection; Banziger et al. 2000). The other issue of interest is if indirect selection for specific traits in an early-growth stage in controlled pot trials is a viable option for pearl millet breeding targeting grain yield (GY) performance under low-P field conditions. This is the first study to examine genetic variation of pearl millet under field conditions in several locations of WA under varying P-levels and also at early-growth stage under pot conditions with varying P-levels.

Plant responses to phosphorus deficiency and target traits for pearl millet phosphorus efficiency in WA

Phosphorus concentration in the soil solution is usually much less than 0.3 mg P L^{-1} and often as low as 0.001 mg P L^{-1} whereas concentrations in plant tissues could be as high as 300 mg P kg^{-1} (Bieleski 1976; Manske et al. 2000) with P uptake always being against the concentration gradient. A series of responses are initiated in a plant under P deficiency for enhancing P efficiency by either enhancing the efficiency with which a plant takes up P from the soil (P-uptake efficiency) or the efficiency with which the plant internally utilizes the P taken up (internal P-utilization efficiency; Hammond and White 2008; Richardson et al. 2011). Responses towards P-uptake efficiency involve altered root morphology and architecture (Lynch and Brown 2001; Lynch 2007), exudation of carboxylates (Lambers et al. 2006, 2011), secretion of phosphatases (Vance et al. 2003; Richardson et al. 2009) and forming symbioses with arbuscular mycorrhiza (Smith and Read 2008). Internal P-utilization efficiency on the other hand involves faster growth and greater allocation of biomass to harvestable parts (Veneklaas et al. 2012). These strategies have been said to be potentially independent and may offer additive benefits if they co-exist in the same genotype (Richardson et al. 2011) which would be of particular importance for WA where soils are low in total P, with possibly high P-fixation capacity and with low P-fertilizer use (Hash et al. 2002; Kochian 2012; Obersteiner et al. 2013). This is because P-uptake efficiency has been proposed for soils with these characteristics but P-uptake efficiency alone though beneficial to grain yield (Rose and Wissuwa 2012) would lead to further soil mining if the P taken up is not replenished (Veneklaas et al. 2012). An excellent P-utilization efficiency in combination with P-uptake efficiency seems therefore highly recommendable for WA. This is the first study to examine in pearl millet the genetic variation for and the relationship between P-uptake efficiency, internal P-utilization efficiency and grain yield from independent environments in WA.

The genetics underlying performance under low-phosphorus conditions

Although crop improvement under abiotic stress has been achieved in the past through the manipulation of QTLs, there is increasing need for further genetic dissection of the QTLs controlling the adaptive responses of crops to abiotic stresses in order to apply genomic-based approaches to plant breeding (Collins et al. 2008). This requires proper estimation of positions and effects of QTLs. Since the 1990s efforts have been directed towards mapping QTLs for P efficiency with more efforts being directed towards P-uptake efficiency since it has a higher correlation with grain yield under field conditions compared to internal P-utilization efficiency (Rose and Wissuwa 2012). As a result, several QTLs related to P efficiency have been reported in crop plants including maize (Reiter et al. 1991; Chen et al. 2009, 2011; Li et al. 2010; Zhang et al. 2014; Mendes et al. 2014), rice (Wissuwa et al. 1998; 2002) soybean (Li et al. 2005) and common bean (Yan et al. 2001; Beebe et al. 2006). A few of these QTLs have been validated and the underlying genes identified. For instance, Gamuyao et al. (2012) showed that *PSTOL1* (*phosphorous-starvation tolerance 1*), a gene encoding a protein kinase, enhances early root development in rice thus improving P-uptake efficiency and, ultimately, increasing grain yield under P deficiency. This gene underlies a QTL named *PUP-1* first mapped by Wissuwa et al. (1998). Homologues of *PSTOL1* have also been reported to be associated with early-shoot P uptake, shoot biomass production and higher grain yield under low-P conditions in WA sorghum (Leiser et al. 2014) and to P-uptake efficiency, root architectural traits and grain yield in a genetically independent sorghum mapping populations in Brazil (Hufnagel et al. 2014). In addition to the *PSTOL1* homologues, Leiser et al. (2014) also identified a co-location of genomic regions responsible for grain yield performance under low-P conditions and aluminum (Al) tolerance through genome-wide association mapping. In maize, several genes responsible for root development and morphology have been reported (Lim et al. 2005; Wen et al. 2005; Brady et al. 2006; Taramino et al. 2007; Hochholdinger et al. 2008) and a few of them have been validated by de Souza et al. (2012). This is the first study to examine molecular markers associated with P-related traits and grain yield performance under low-P field conditions in pearl millet.

Study objectives

The present study therefore sought to achieve the following specific objectives aimed towards exploring the prospects of improving pearl millet grain yield under low-P conditions in WA:

1. To estimate quantitative-genetic parameters for grain yield of a wide range of WA pearl millet open-pollinated varieties, inbred lines and testcrosses under contrasting P-fertilization levels in multi-location field trials in order to establish a selection strategy for pearl millet targeting P-limited environments;

2. To establish the relationship between P efficiency adaptive traits and grain yield in order to make inferences on which target traits should be considered in adapting pearl millet to low-P conditions in WA; and
3. To identify genetic polymorphisms underlying quantitative traits under P-limited conditions based on diversity array technology (DArT) markers.

Inbred and Testcross Performance under Low Phosphorus in West African Pearl Millet

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Abstract

Pearl millet [*Pennisetum glaucum* (L.) R. Br] is a food security crop for millions living in drylands of Africa and Asia. Its production on acid sandy soils of the Sahel is limited by erratic rainfall and poor soil fertility, especially low-phosphorus (P) soils. We sought to elucidate the genetic variation in West and Central African landrace-derived inbred lines for grain yield under low-P conditions, to determine their performance as inbred lines *per se* and in hybrid combinations, and to determine quantitative-genetic parameters in order to derive an appropriate breeding strategy so as to enhance grain yield under low-P conditions. We evaluated a total of 155 landrace-derived inbred lines as well as their testcrosses in four locations over two years under two treatments, high-P (HP; with P fertilization) and low-P (LP; without P fertilization). Results revealed significant effects for genotypes, P-level, genotype × P-level, as well as genotype × environment interactions. Grain yield reductions under LP treatment ranged from 7.9 to 35.5%, and 11.2 to 60.9% for inbred lines and testcrosses respectively, with positive mid-parent heterosis averaging 43.5% under LP. We conclude that direct selection of testcrosses under LP is more effective and that indirect selection for testcross performance from inbred line performance is not desirable.

Gemenet D.C., Hash C.T., Sy O., Zangre, R.G., Sanogo, M.D., Leiser W.L., Parzies H.K. and Haussmann B.I.G. (2014). Pearl millet inbred and testcross performance under low phosphorus in West Africa. Crop Sci. 54:2574–2585.

Phosphorus Uptake and Utilization Efficiency in West African Pearl Millet Inbred Lines

Dorcus C. Gemenet, C. Tom Hash, Moussa D Sanogo, Ousmane Sy, Roger G. Zangre, Willmar L. Leiser and Bettina I.G. Haussmann*

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Abstract

Pearl millet [*Pennisetum glaucum* (L.) R. Br] production on the acid sandy Sahelian soils in West Africa (WA) is severely limited by low plant-available phosphorus (P) in addition to erratic rainfall. We sought to examine the genetic variability for P-uptake and P-utilization efficiency in 180 WA pearl millet inbred lines or subsets thereof under low-(LP) and high-P (HP) conditions in one field and two pot experiments, determine the relationships among the measured traits and grain yield under field conditions at three other independent WA sites, and identify potential secondary selection traits for improving grain yield under LP. We observed genetic variation for P-uptake and utilization in both seedling and mature plants. P-utilization efficiency increased under LP conditions. Total P-uptake was more important for grain production than P-utilization under LP field conditions (r = 0.57*** vs r = 0.30***). The estimated response to indirect selection was positive for most of the measured morphological and P-efficiency parameters. We conclude that both seedling and mature plant traits are potentially useful as secondary traits in selection of pearl millet for low-P adaptation. These results should be validated using heterozygous pearl millet genetic materials. Ultimately, pearl millet breeding activities for low-P tolerance in WA should be integrated with other system-oriented research such as nutrient cycling, intercropping or rotations with legumes, better crop-tree-livestock integration, and modest applications of locally available rock phosphate.

Gemenet D.C., Hash C.T., Sanogo M.D., Sy O., Zangre R.G., Leiser W.L. and Haussmann B.I.G. (2015a). Phosphorus uptake and utilization efficiency in West African pearl millet inbred lines. Field Crops Res. 171:54–66.

Towards Understanding the Traits Contributing to Performance of Pearl Millet Open-pollinated Varieties in Phosphorus-limited Environments of West Africa

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Abstract

Aims: Pearl millet [*Pennisetum glaucum* (L.) R. Br.] open-pollinated varieties, which are the predominant cultivars, have never been systematically evaluated for adaptation to low-soil phosphorus (P), a major constraint on pearl millet production in West Africa (WA).

Methods: We evaluated grain yield (GY), flowering time (FLO), harvest index (HI), and residual grain yields (RGY) of 102 open-pollinated varieties from WA under low-P (–P) and high-P (+P) field conditions in six environments of WA. In addition, PE-related traits of the varieties were evaluated at early growth stage in a pot experiment.

Results: Significant genetic variation was observed for GY, FLO, HI and PE-related traits. P-efficient varieties had higher yield under –P conditions. Varietal performance under –P varied across environments depending on FLO, relative flowering delay under –P (FD) and RGY measured in the field. Low-P-susceptible varieties had higher FLO, lower HI than low-P-tolerant varieties. Response to direct selection under –P field conditions was 20.1 g m^{-2}, whereas indirect selection response under +P was 16.3 g m^{-2}.

Conclusions: Selection under –P field conditions while taking into account seasonal variations for FLO, FD and PE is expected to be important for improving GY specifically targeting –P environments in WA.

Gemenet D.C., Beggi F., Hash C.T., Sy O., Sanogo M.D., Zangre R.G., Falalou H., Buerkert A. and Haussmann B.I.G. (2015b). Towards understanding the traits contributing to performance of pearl millet open-pollinated varieties in phosphorus-limited environments of West Africa. Plant Soil, DOI 10.1007/s11104-015-2636-9

Association Analysis of Low-Phosphorus Tolerance in West African Pearl Millet using DArT Markers

Dorcus C. Gemenet, Willmar L. Leiser, Roger G. Zangre, Ignatius I. Angarawai, Moussa D. Sanogo, Ousmane Sy, Thudi Mahendar, C. Tom Hash and Bettina I.G. Haussmann*

The final publication is available at Springer via http://dx.doi.org/10.1007/s11032-015-0361-y

Abstract

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is a food security crop in the harshest agricultural regions of the world. While low soil-phosphorus (P) availability is a big constraint on its production, especially in West Africa (WA), information on genomic regions responsible for low-P tolerance in pearl millet is generally lacking. We present the first report on genetic polymorphisms underlying several plant P-related parameters, flowering time (FLO) and grain yield (GY) under P-limiting conditions based on 285 diversity array technology (DArT) markers and 151 West African pearl millet inbred lines phenotyped in six environments in WA under both high-P and low-P conditions. Nine markers were significantly associated with P-related traits, nine markers with FLO whereas thirteen markers were associated with GY each explaining between 5.5 % and 15.9 % of the observed variation. Both constitutive and adaptive associations were observed for FLO and GY, with markers *PgPb11603* and *PgPb12954* being associated with the most stable effects on FLO and GY, respectively, across locations. There were a few shared polymorphisms between traits, especially P-efficiency-related traits and GY, implying possible co-location of genomic regions responsible for these traits. Our findings help bridge the gap between quantitative and molecular methods of studying complex traits like low-P tolerance in WA. However, validation of these markers is necessary to determine their potential applicability in marker-assisted selection programs targeting low-P environments, which are especially important in WA where resource-poor farmers are expected to be the hardest hit by the approaching global P crisis.

Gemenet D.C., Leiser W.L., Zangre R.G., Angarawai I.I., Sanogo M.D., Sy O., Mahendar T., Hash C.T. and Haussmann B.I.G. (2015c). Association analysis of low-phosphorus tolerance in west african pearl millet using DArT markers. Molecular Breeding 35: 171. DOI 10.1007/s11032-015-0361-y

General Discussion

Selection strategy for pearl millet under low-P conditions in WA

Results were presented based on evaluation of three different genotype groups in multiple site-season combinations and two P-levels: nearly homozygous inbred lines, their heterozygous testcrosses (Gemenet et al. 2014; Gemenet et al. 2015a) and heterozygous, heterogeneous open-pollinated varieties which represent the natural state of commonly grown pearl millet varieties in WA (Gemenet et al. 2015b). Due to a low correlation between performance of inbred lines and testcrosses, direct selection of testcrosses for performance under low-P conditions was found to be 44% more efficient than indirectly selecting for testcross performance based on inbred lines' performance This is because the gene effects in the inbred lines are mainly additive in nature with less environmental interaction than the gene effects in the testcrosses which are mainly dominant and prone to more environmental interaction (Holland 2001), evidenced in the current study by the higher broad-sense heritability observed for inbred lines than for testcrosses. Therefore selection strategies mainly apply to testcrosses and open-pollinated varieties.

Wide versus specific adaptation

A differential phenotypic response of genotypes to changing environments, i.e., presence of G x E interaction (Vargas et al. 2001) reduces the genetic progress expected from plant breeding. Proper definition of the amount and type of G x E interaction aids in decision making with regard to the adaptation method in breeding, and recommendation domains for new varieties identified (Yan and Hunt 2001; Yan 2011; Tolessa et al. 2013). We observed substantial G x E interaction in our field evaluations; however further dissection of the G x E using GGE biplots (Yan and Kang 2002) showed that most of the observed G x E interaction was caused by only few locations while genotypes were ranked relatively the same in most of the other site-season combinations (Gemenet et al. 2014, 2015b, 2015c). For instance, only Bambey 2010 formed a distinct mega environment for the open-pollinated varieties (Gemenet et al. 2015b). Since the low-P field evaluations within the region were started in 2010, it is possible that a new field with a higher organic matter content was used in Bambey 2010. The fact that most site-season combinations were representative of each other (genotypes ranked similar among them), indicates that it is possible to select varieties targeting a wide range of environments within the region (Finlay and Wilkinson 1963; Allard and Bradshaw 1964). Furthermore, no distinct mega-environments were observed in relation to P-levels within the site-season combinations indicating that the P situation was relatively uniform within the region. However since there was some significant G x E interaction of cross-over type for a few locations, it means that both wide and specific adaptation could be pursued in future. The decision on which adaptation method to emphasize will depend on the clear definition of breeding objectives and the target environment for which improvement is aimed. Since we evaluated each of the three genotype groups for two years only, it may be necessary to continue evaluation for more years in order to conclusively comment on yield stability of the selected genotypes.

Direct versus indirect selection for low-P conditions

In breeding activities targeting stress environments, decisions must be made on whether to select genotypes directly under stress conditions or indirectly under non-stress conditions. The decision is mainly based on the genetic correlation between genotypic performance under the two types of environment and the heritability in each environment (Falconer 1952; Atlin and Frey 1989). If the selection intensity can be substantially lower e.g. under non-stress or controlled conditions, this can be an additional aspect to be considered. In the current study, we observed consistently high genetic correlation (r_g) between low-P and high-P treatments; ranging from $0.87 \leq r_g \leq 0.98$ in inbred lines, $0.81 \leq r_g \leq 0.90$ in testcrosses (Gemenet et al. 2014) and $0.63 \leq r_g \leq 0.91$ in open-pollinated varieties (Gemenet et al. 205b). These genetic correlation ranges are somehow comparable to those reported in WA sorghum $0.5 \leq r_g \leq 0.99$ (Leiser et al. 2012) but are rather higher compared to those reported in other crops such as oats, maize and rape seed (Atlin and Frey 1989; Parentoni et al. 2010; Ding et al. 2012). Furthermore, response to direct selection under low-P conditions in open-pollinated varieties was 20.1 g m^{-2} whereas response to indirect selection under high-P conditions was 16.3 g m^{-2}. Pearl millet is the hardiest crop among all cereals and smallholder farmers grow it under very low-input conditions with seed being the only major input allocated to its production apart from management and labor (Ndjeunga 2002; Mariac et al. 2006; Supriya et al. 2011). It is therefore only fair to say that pearl millet is generally adapted to these low-input conditions including low-soil P. This explains the consistently high genetic correlations between high- and low-P conditions observed for the different genotype classes in the present study. Whereas the observation of high genetic correlations and the minimal difference in response to selection under high-P and low-P conditions suggest that genotypes can be indirectly selected under high-P conditions for performance under low-P, we however observed significant genotype-by-P-level interaction (G x P) of crossover type in most genotype classes (Gemenet et al. 2014, 2015b) indicating that some genotypes were specifically adapted to low-P conditions and indirect selection of genotypes under high-P conditions would leave out such genotypes. For instance 40% of the selected open-pollinated varieties and 53% of the selected testcrosses showed specific adaptation to low-P conditions. Among the open-pollinated varieties (Gemenet et al. 2015b), the highest yielding variety under low-P conditions was an original landrace (PE00077) which also showed specific adaptation to low-P. Among the improved open-pollinated varieties selected for higher grain yield under low-P were Serkin_C2_Kandela_SMS and Doga_C2_PF_comb both improved by farmer-participatory breeding conducted on-farm with women in Niger in their low-input fields. Selection in this genotype group (open-pollinated varieties) was of more importance in this study since such varieties could be directly recommended to smallholder farmers for low-P conditions. Furthermore, direct selection under low-P conditions was 28% and 39% more efficient than indirect selection under high-P conditions for testcrosses and open-pollinated varieties, respectively (Gemenet et al. 2014, 2015b). It is sometimes believed that direct selection under stress might reduce response to selection because of reduced heritability and increased error (Ceccarelli 1989; Atlin and Frey 1990). However, several studies have shown that germplasm evaluation under low-P or stress conditions can achieve the same precision as evaluation under high-P or non-stress conditions, with the actual heritability estimates also depending on the type of germplasm (robust landraces *versus* less robust “improved” materials) included in the study (Ceccarelli 1996; Burger et al. 2008; Leiser et al. 2012). In the present study, the differences between broad-sense heritability under low-P and high-P conditions were not statistically significant (0.57 versus 0.62 for testcrosses; 0.75 versus 0.78 for inbred lines and 0.73 versus 0.77 for open-pollinated varieties; Gemenet et al. 2014; 2015b). This suggests that direct selection under low-P conditions did not reduce selection precision. For breeding activities targeting low-P environments in WA smallholder farms, it is therefore important that selection of genotypes be done under low-P conditions. However since soil management practices may differ from farmer to farmer, breeding activities should be planned depending on proper definition of soil type, soil P reserves and other soil fertility maintenance practices common in the target environment. This therefore suggests that breeding activities could be specifically adapted through participatory approaches involving the target farmers (Haussmann et al. 2012). For instance, two improved open-pollinated varieties derived from farmer-participatory breeding were found superior under low-P conditions in the present study (Doga_C2_PF_comb and Serkin_C2_Kandela_SMS). Serkin_C2_Kandela_SMS showed specific adaptation to low-P conditions, whereas Doga_C2_PF_comb had wide adaptation and superior yield in both low- and high-P conditions (Gemenet et al. 2015b). This reflects the diversity of farmer preferences. The fact that the Doga variety revealed wide adaptation to both low- and high-P conditions indicates an opportunity for selecting fertilizer-responsive genotypes with good adaptation to low-P conditions, thereby serving both resource-poor farmers and farmers who can afford to provide fertilizer inputs.

Indirect selection under pot trial conditions for field performance

The following factors determine the applicability of physiological traits such as those measured in early growth stages in pot trials as secondary (indirect selection) traits to select for higher GY under field conditions: genetic correlation of the physiological traits with GY, extent of genetic variation, heritability estimates and G x E (Mir et al. 2012). We evaluated the correlation between performance under pot conditions to GY under field conditions as well as the expected response to selection under pot and low-P field conditions. Low genetic correlation as well as lower absolute yield increases and lower responses to selection were observed in the current study (Gemenet et al. 2015a, 2015b). Low genetic variation and low heritability have also been reported for sorghum evaluations in pot conditions for resistance to the parasitic weed *Striga hermonthica* (Del.) Benth. (Omanya et al. 2004). The difficulty of extrapolating results measured in pots to performance under field conditions has been alluded to by several authors (Passioura 2006; Salekdeh et al. 2009; Poorter et al. 2012a, 2012b), and is mainly a result of the dynamism of the phenotype in response to the various endogenous and exogenous stimuli over the growing period in the field (Houle et al. 2010; Cobb et al. 2013), and the limited, artificial rooting environment in a pot trial (Omanya et al. 2004). This therefore implies limited applicability of pot experiments to select genotypes for performance under field conditions in WA pearl millet and implies that such decisions about potential indirect selection methods must be made considering availability of financial resources, time, selection intensity, heritability, expected response from selection and the target region (Gemenet et al. 2015a, 2015b). For instance, if there are a lot of genotypes to be evaluated and enough financial resources, then rapid evaluation of the genotypes could be done in pots for simple non-destructive traits like plant height which had a higher correlated response to GY under low-P conditions than other traits measured in pots in the present study. The reduced number of selected genotypes can then be evaluated under field conditions in target environments for final selection.

Target traits in adapting pearl millet to low soil phosphorus in WA

Phosphorus efficiency, defined as the yield per P supplied from the soil or fertilizer (Manschadi et al. 2014), can be divided into P-uptake efficiency and P-utilization efficiency (Moll et al. 1982; Wang et al. 2010). Pearl millet inbred lines from WA were evaluated for P-uptake efficiency and P-utilization efficiency at early growth stage in pots as well as under field conditions (Gemenet et al. 2015a). Open-pollinated varieties were also evaluated for the same P-efficiency and interaction with mycorrhiza at early-growth stage under pot conditions (Beggi et al. 2014a, 2014b) as well as performance under field conditions (Gemenet et al 2015b). A wide genetic variation exists in WA pearl millet for the two mechanisms and indicates an opportunity for improving these two mechanisms. P-uptake efficiency especially under field conditions was more associated with GY under low-P than P-utilization efficiency. Drought stress confounds P-efficiency under field conditions and flowering time and flowering delay under low-P stress are important considerations in addition to genotypic P-efficiency in adapting pearl millet to low-P conditions in WA.

Phosphorus-uptake efficiency

Most WA soils have low total soil P and possibly a high P fixation rate although the P fixation capacity needs to be validated further in the acid sandy soils of Sahelian WA (Andreas Buerkert, Personal communication). The soil mineral properties in this region have also been shown to enhance mineral toxicities for instance Al and/or Mn toxicities and mineral deficiencies for instance K, Ca, and/or Mg deficiencies (Scott-Wendt 1988). The interaction among these soil properties, drought and P availability is exemplified in the present study by minimal differences between genotypic means under low-P and high-P conditions, despite addition of substantial amounts of P to the high-P treatment (Gemenet et al. 2014, 2015a, 2015b, 2015c). It is therefore important that a genotype in such soils is able to efficiently take up the plant available P supplied in form of fertilizer or manure (root foraging) or be able to mobilize and use the unavailable forms of P in the soil (P mining; Manske et al. 2000; Hash et al. 2002; Beebe et al. 2006; Richardson et al. 2009; Wang et al. 2010). Important traits for foraging would be variation in root morphology and architecture as well as forming symbioses with arbuscular mycorrhiza (AM; Richardson et al. 2011). Genetic variation in root traits, although not directly studied in the present study might result in genetic variation for P-uptake. Brück et al. (2003) reported a high variability of root traits in pearl millet under low-P field conditions in Niger and proposed indirect selection for root traits using shoot traits. Beggi et al. (2014b) showed a positive correlation between early mycorrhization, increased amount of AM, a higher total root length infected with AM and a higher P-uptake efficiency in low-P tolerant open-pollinated varieties under low-P conditions. This confirms genetic variation and a beneficial effect for AM infestation in pearl millet (Bielders et al. 2010) and presents an opportunity for pursuing this mechanism of improving P-uptake efficiency in WA pearl millet. However, these studies were carried out under pot conditions whereas pearl millet under field conditions grows under a combination of stresses (e.g. P and water stress) with unique genotypic responses to these combined stresses that cannot be extrapolated from responses to each stress separately (Hash et al. 2002; Mittler 2006; Atkinson and Urwin 2012; Manschadi et al. 2014). Furthermore, the reported beneficial effect of AM in pearl millet is contrary to what was reported for WA sorghums where early mycorrhization had a negative influence on biomass and P-uptake efficiency (Olatoye 2013) and was not related to final grain yield performance (Leiser et al. 2015).

Trade-offs have been reported for P-uptake efficiency-related root traits (shallower foraging root systems) and water-uptake root traits (deeper root systems; Ho et al. 2005; Lynch 2011; Manschadi et al. 2014). Further research is therefore needed to understand the genetic variation for pearl millet root systems under field conditions, to be able to identify possible genotypes with dimorphic rooting systems able to permit vigorous root growth both in the surface and deeper soil horizons. The AM mechanisms should also be examined under these field interactions. The soil P mining approach has to do with exudation of organic anions like carboxylates and phosphatases (Lynch 2007; Richardson et al. 2009, 2011) with a double benefit for Al tolerance and P-uptake efficiency. This is still an area that could be pursued further for genetic variation in WA pearl millet under low-P field conditions.

Phosphorus-utilization efficiency

Whereas P-uptake efficiency is very important under the WA soil characteristics, the low level of P-fertilizer use in WA complicates matters more and has the potential of making the pearl millet production system unsustainable if only P-uptake efficiency is targeted. Genotypes targeting low-P environments in smallholder farms in WA therefore should combine both P-uptake and P-utilization efficiencies (Rose et al. 2011; Gemenet et al. 2015a, 2015b). P-utilization efficiency as a trait was positively correlated with GY under low-P field conditions and not associated with P-uptake in pearl millet, therefore implying that improving one trait had no effect on the other (Gemenet et al. 2015a). However P-utilization efficiency as a trait is compounded by both P-uptake efficiency and grain harvest index (Rose et al. 2011; Gemenet et al. 2015a). Furthermore, internal P-utilization efficiency has to do with partitioning of the P taken up to the harvestable parts of the plant (Veneklaas et al. 2012). For instance, about 60% of the P taken up by pearl millet under low-P in the present study was apportioned to the grain (Gemenet et al. 2015a). This signifies a large loss of P from the farming systems which is expected to increase further with targeted breeding for P-uptake efficiency. Trade-offs have also been reported between the need to increase GY by increasing P-uptake efficiency and zinc, iron and calcium bioavailability in human nutrition due to a higher content of phytate associated with a higher P-uptake efficiency (Buerkert et al. 1998; Manschadi et al. 2014). Targeted breeding for lower P concentration in grains has been proposed as one approach to try and reduce the P losses from the farming systems as well as tackle the micronutrient deficiency caused by higher phytate and associated lower micronutrient bioavailability levels in the grains (Rose et al. 2010, Leiser et al. 2014, Gemenet et al. 2015a). This would be of interest to WA where low-soil P is a problem and where micronutrient deficiencies ("hidden hunger") are prevalent. However, there are several trade-offs identified here. First is the impact of reducing seed P content on germination, seedling establishment and final grain yield of the next generation (Raboy 2009; Robinson et al. 2012; Rose et al. 2012). Second is the effect of reducing P content in grains on human nutrition since P is also the most abundant mineral in the human body and a substantial amount of it is consumed through cereals (Welche et al. 2009; Rose et al. 2013). Third is the effect of targeted reduction of phytate P in the grain in order to make iron and zinc more bioavailable whereas phytate P has also been shown to have beneficial effects against cancer, diabetes mellitus, atheroscelerosis and heart diseases (Kumar et al. 2010; Rose et al. 2013). Lastly would be the effect of reduced P content on DNA composition since the P:N ratio in DNA is conserved and reducing amount of P may disrupt this conservation (Rose et al. 2013; Manschadi et al. 2014). Research is therefore necessary in pearl millet to explore the possibility and trade-offs of the option of reduced P concentration in grain and/or targeted reduction in grain phytate P as an approach towards attaining internal P-utilization efficiency. For instance, there is need to validate the relationship between grain P concentration and seedling vigor and to examine the possibility of increasing other P forms e.g. phospholipids and lysophospholipids in the grains which have direct benefits to human nutrition at the expense of phytate P.

Flowering time

Low-P stress leads to a P-deficiency induced delay in flowering with the hope that a plant will catch up with P-uptake if the delay in flowering is long enough. This would then imply that plants with a longer flowering delay under low-P conditions would be more tolerant to low-P conditions (Nord and Lynch 2008). However, for WA conditions with erratic rainfall and unpredictable droughts, we did not observe significant difference in flowering delay (FD) between tolerant (10 best genotypes for grain yield under low-P) and susceptible (10 worst genotypes for grain yield under low-P) genotypes under low-P conditions indicating a confounding effect of drought stress on P-efficiency with regard to flowering delay under low-P. For instance, a genotype having a longer delay under low-P conditions but which is susceptible to drought stress would have a lower grain yield if terminal drought stress occurred compared to one with no delay or one with a shorter delay under low-P conditions. This inference was based on the observation that early flowering was positively associated with grain yield under both low-P and high-P conditions in most of the evaluation environments thus implying that water availability played an important role with regard to grain formation in WA pearl millet (Gemenet et al. 2015b). This was also supported by the fact that in the highest yielding environment, Bambey 2010 which was clearly separated from the others, late flowering was positively correlated with grain yield under low-P thus implying that the relationship between flowering time and grain yield under low-P was under the control of another major factor besides low-P, in this case, water availability. P-uptake reduces to near zero during drought stress (Hash et al. 2002; Sinclair and Vadez 2002) and this is supported in the current study by the lack of strong genotypic diferences between low-P and high-P treatments despite addition of substantial amounts of P to the high-P treatments (Gemenet et al. 2014, 2015a, 2015b and 2015c). What is important to note is that there was genetic variation for flowering time under low-P, flowering delay under low-P and residual grain yield under low-P (an estimate of P-efficiency excluding yield potential; Gemenet et al. 2015b) implying that each of this traits can be improved in WA pearl millet. With regard to flowering also, photoperiod sensitivity has been said to have a possible role in plants' adaptation to low-P stress including *Arabidopsis* (Nord and Lynch 2008) and sorghum (Clerget et al. 2008; Leiser et al. 2014b). It is therefore important to consider all these factors when adapting pearl millet to low-P environments of WA. Further studies on the interactions among photoperiodism, low-P adaptation and drought-stress adaptation are necessary in pearl millet to better understand the observed variations for low-P adaptation across environments.

Genetic polymorphisms underlying low-P tolerance in pearl millet

Given the difficulty associated with field evaluation for low-P tolerance as evidenced in this study, marker-assisted selection would help expedite the breeding process and get tolerant varieties to the farmers faster. This is of particular importance in WA where smallholder resource-poor farmers are expected to be the hardest hit by the global P crisis (Cordell et al. 2009; Obersteiner et al. 2013). Being an ‘orphan’ crop however, marker assisted breeding in pearl millet is not quite as advanced as in other cereals and in fact the first marker-assisted selection product was only released as late as 2005 (Hash et al. 2006). Nevertheless efforts have been made in the field especially towards dissecting QTLs responsible for drought tolerance (Yadav et al. 2002, 2003, 2004, 2011; Serraj et al. 2005; Bidinger et al. 2007; Sehgal et al. 2012). To the best of our knowledge, this is the first study to specifically look at genomic regions responsible for low-P tolerance in pearl millet.

Using 285 DArT markers, we were able to identify several polymorphisms associated with P-uptake, P concentration in stover and grain, P-utilization efficiency, days to flowering as well as grain yield, individually explaining from 5.5 % to 15.9 % of the observed variation in the respective traits (Gemenet et al. 2015c). This is evidence that low-P tolerance in pearl millet is a complex trait under the influence of many genes and different adaptation mechanisms. Quantitative trait loci for P-efficiency-related traits have been reported in many major crops (Gemenet et al. 2015c). Under low-P field conditions as applied in the current study, Mendes et al. (2014) identified six QTLs associated with P-uptake efficiency and five QTLs associated with P-utilization efficiency in maize. Flowering time is a major adaptive trait in pearl millet (Stich et al. 2010). Our observation albeit by chance that most marker-trait associations for FLO identified in the current study were related to early flowering is in line with findings of other studies in pearl millet. For instance Saidou et al. (2009, 2014) showed that the region around PHYTOCHROME C (PHYC) gene is responsible for flowering time in pearl millet and identified an early flowering allele within the PHYC region. Similarly, Anand Kumar and Andrews (1993) showed that photoperiod-insensitive early flowering in pearl millet was controlled by two independently segregating, recessively inherited genes, e_1 and e_2. The genetics underlying grain yield performance under P-limited conditions have also been recently reported in sorghum (Leiser et al. 2014; Hufnagel et al. 2014) and maize (Mendes et al. 2014). Based on the approach we followed of capturing both specific and multiple effect polymorphisms, we were able to identify both constitutive (consistent across several environments) and adaptive (detected only in specific environments) polymorphisms (Collins et al. 2008). For instance, PgPb11603 was a constitutive polymorphism for early flowering - a positive effect to be selected for, whereas PgPb112954 was a constitutive polymorphism whose presence led to inreased grain yield and should therefore also be selected for. Via et al. (1995) proposed that genetic control of trait stability in multiple environments could be either due to the regulation of the constitutive gene itself in direct response to the environment, also referred to as the allele sensitivity model or where regulatory loci are under the direct influence of the environment and they in turn switch on and off the constitutive genes. It is not possible to tell with our current result which of these was under play. The lack of association of most polymorphisms with specific performance either under low-P or high-P conditions indicates that the two treatments in our field evaluation were actually P-limited and explains the minimal differences between low-P and high-P means as observed in field evaluations (Gemenet et al. 2015c). A few markers were associated with more than one trait. For instance, marker *PgPb7101* had significant association with P concentration in stover, P-uptake and P-utilization effciency and grain yield. We cannot tell with the current findings if these shared polymorphisms are the result of pleiotropy or tight linkage (Lebreton et al. 1995; Tuberosa et al. 2002; Saidou et al. 2014). The result of possible co-location of genetic polymorphisms for P-uptake efficiency and grain yield are in line with the findings reported in sorghum (Hufnagel et al. 2014; Leiser et al. 2014). The main limitation of the current study is the lack of information concerning the genomic positions of the identified polymorphisms since most of the identified markers were not found on the genetic map by Supriya et al. (2011) which integrates DArT and simple sequence repeat (SSR) markers. This makes it difficult to compare the current results with already reported QTLs and/or genes in pearl millet. There is therefore need to sequence the DArT clones upon which marker-trait associations identified in this study are based in order to overcome this limitation. This will specifically be facilitated by the pending release of the aligned pearl millet genome sequence.

The findings of subtle population structure and little familial relatedness reported in the current study based on landrace-derived inbred lines, supported by the findings of Baskaran et al. (2009, 2014) based on full-sib progenies of random mating populations indicate potential for marker-assisted population breeding in allogamous pearl millet. For them to be useful in bridging the gap between quantitative and molecular methods of studying adaptation to low-P conditions in WA pearl millet systems, there is need for validation of these polymorphisms. Given the recently sequenced but yet unpublished pearl millet draft genome, there is also an opportunity to re-examine these genetic polymorphisms using single nucleotide polymorphisms (SNPs) obtained from either whole genome sequencing or candidate genes.

Prospects for pearl millet hybrid breeding in West Africa

This was the first study to evaluate single-cross testcrosses in WA pearl millet which have the ability to exploit maximum heterosis. Testcrosses were significantly superior over inbred lines and partially superior over open-pollinated checks under both low- and high-P conditions, indicating the potential usefulness of pearl millet hybrid breeding in WA (Gemenet et al. 2014). In India, pearl millet single-cross hybrids are already widely grown, especially in higher-yielding environments (Govila et al. 1997). However, pearl millet in WA grows under conditions of unpredictably variable drought, high temperatures and poor soils with a lot of interactions among these factors (van Staveren and Stoop 1985; Payne et al. 1998). The amount of phenotypic plasticity or capacity to buffer unpredictable environmental heterogeneity can be expected to be too narrow in uniform single-cross hybrids, considering the highly variable and changing growing conditions in WA (Haussmann et al. 2012). Genetically more heterogeneous hybrid variety types such as population or topcross hybrid varieties might be preferable. Previous studies have shown significant superiority of pearl millet population hybrids over popular landraces (Ouendeba et al. 1993; Haussmann 2009). These hybrid variety types do also have the advantage that farmers can re-use the seed due to the absence of inbreeding depression in the following generation (as opposed to re-growing single-cross hybrids) and are therefore more appropriate for smallholder farmers in WA where seed systems are not yet well established (Haussmann et al. 2012).

One limitation of our study in relation to pearl millet hybrid breeding was the fact that the testcrosses were all produced on only one tester, chosen based on availability of enough seed to make the crosses, but without knowing its heterotic grouping (Gemenet et al. 2014). More systematic efforts are required for proper definition of heterotic pools in WA pearl millet germplasm, in order to establish a sound and sustainable basis for future hybrid breeding. Nevertheless, the present results indicate potential for further exploiting heterosis in WA pearl millet. These preliminary results could serve as a basis to observe some combining ability patterns that can inform heterotic grouping in WA pearl millet by correlating the combining ability of the inbred lines used in the present study towards the tester with the genetic distance between the inbred lines and the tester. Plans are underway in WA pearl millet breeding towards establishment of heterotic groups in a follow up project named ‘Bringing the benefits of heterosis to smallholder sorghum and pearl millet farmers in West Africa’ which runs from 2014 to 2017.

Conclusions and implications for pearl millet breeding activities targeting low-phosphorus environments

Being the first study targeting low-P tolerance in WA pearl millet, the findings from the current study offer new insights for breeding activities aiming to improve P efficiency in pearl millet. The following conclusions can be drawn from these findings:

- There is significant genetic variation for pearl millet performance under low-P conditions hence genetic improvement of pearl millet for P-limited environments in WA should be possible
- Both wide and specific adaptation can be followed in breeding pearl millet varieties for low-P conditions in WA
- Direct selection of pearl millet under low-P conditions should be carried out in breeding activities targeting low-P environments
- Landraces offer a valuable resource for improving pearl millet targeting low-P environments
- A combination of classical, molecular and farmer-participatory breeding might be most efficient towards developing varieties targeting low-P environments
- Indirect selection under pot trial conditions for field performance has limited applicability in pearl millet breeding activities targeting low-P field conditions
- There is potential for further exploitation of heterosis in WA pearl millet using more heterogenous hybrids like 3-way cross, double cross or top cross hybrids when proper heterotic grouping is done.
- There is a substantial genetic variation for both P-uptake and P-utilization efficiency among pearl millet genotypes in WA and hence genetic improvement for either mechanism is possible.
- P-uptake efficiency is more correlated to grain yield in WA than P-utilization efficiency and given the interactions among P, drought and other soil characteristics evident within the region, it should be selected for in varieties targeting low-P environments.
- Given the already low-P content of the soils in the region and the low-input conditions, genotypes selected for low-P environments should combine both P-uptake and internal P-utilization efficiency
- A lower P concentration in grain could offer a strategy for improving internal P-utilization efficiency in pearl millet but there is need to properly understand the effects

and trade-offs of this on the next generation crop performance (seedling vigor), human nutrition and DNA composition

- Because of multiple low-P effects and interactions with other environmental factors, low-P tolerance is a polygenic trait with a lot of polymorphisms contributing towards low-P adaptation mechanisms in pearl millet
- There is potential for applying marker-assisted selection approaches in pearl millet breeding activities targeting low-P environments when the polymorphisms identified in the current study are validated.

Outlook for sustainable pearl millet production systems in P-limited environments of WA

The genetic polymorphisms underlying traits related to low-P tolerance in the current study need to be validated in order to establish their applicability in marker-assisted selection targeting low-P environments. This involves testing whether the same marker-trait associations appear when the material is grown in other locations and/or years, and whether the respective effects can still be detected when introduced into a series of different genetic backgrounds thereby ruling out the possibility of statistical anomalies or errors (Landi et al. 2005). However at least for pearl millet, this validation could be achieved more quickly and less expensively by directly selecting for and against specific marker alleles within the inbred lines panel used in the present study, recombination of replicated selected subsets of this inbred panel (that is, groups of inbred lines that either have or do not have the specific presence/absence marker of interest for a given target trait), and replicated field testing of the replicated recombined pairs of sub-populations under high-P and low-P conditions.

Since information concerning the genetic position of most of the markers identified in the current study is lacking, the completion of a draft genome for pearl millet offers a great opportunity to identify genetic polymorphisms underlying low-P tolerance with well-defined map positions for targeted selection. There is therefore need to sequence specific marker clones identified in the current study. Plans are also underway to evaluate the genetic polymorphisms in the inbred lines panel used in the current study based on genotyping-by-sequencing (GBS; Elshire et al. 2011) SNP data called from the draft genome.

Genomic selection which uses all available information to predict genotype performance has been shown to be a promising tool for selecting for grain yield (Meuwissen et al. 2001; Massman et al. 2012; Leiser et al. 2014). The availability of GBS data generated from the inbred lines panel used in the current study offers an opportunity to compare the effectiveness of this genome-wide selection against the selection approaches based on marker-trait associations, in order to make preliminary inferences concerning which molecular approach better suits WA pearl millet improvement targeting P-limited environments.

Given the soil conditions in WA, there is need to enhance genotypic P-uptake efficiency under multiple-stress interaction conditions. Root traits were not specifically studied under this study. Plans are underway to carry out association mapping for root traits at seedling stage of WA pearl millet inbred lines. Whereas this is a welcome idea, there is need to design other field-based studies for such root traits since plant’s responses to combined stresses in the field vary over the developmental cycle (Mittler 2006).

Given the low-input conditions under which pearl millet grows in WA, selecting for P-uptake efficiency only has the capacity to render the production system unsustainable. There is need to combine both P-uptake and internal P-utilization efficiency in the selected genotypes. The proposed strategy of selecting for a lower P concentration in the grain could have other side effects. Studies need to be designed to study the effect of a reduced P in grain on seedling establishment and subsequent grain yield performance. There is also need to establish what could be the effects of reduced P on human nutrition as well as on DNA composition (Rose et al. 2013).

Should such risks be found to be less than the benefits of keeping the production system sustainable, then a higher P-uptake efficiency coupled with a lower P concentration in grain ensures more P in stover to be recycled in the farming systems. There is therefore need to study direct or microbial mediated pathways for genotypic utilization of such P forms including mycorrhizal symbioses, secretion of anions, phosphatase activity among others (Lynch 2007; Richardson et al. 2009, 2011).

Plant breeding does not perform miracles (Haussmann et al. 2012) since breeding mainly seeks to improve the genotype (the G) part of the observed phenotypic variation. There are other non-breeding activities which seek to improve the growing environment (the E) part which are equally important and should be combined with breeding activities targeting low-P environments. Droughts, soil acidity and nutrient depleted and degraded soils are the major constraints on pearl millet production in WA and call for a synergistic provision and conservation of water, nutrients and a supportive soil structure in order to increase productivity (Zougmore et al. 2014). Potential for agronomic enhancement of grain yield in WA is well documented with agronomic practices seeking to replenish or recycle nutrients within the system such as regular amendments with small doses of P fertilizers (Muehlig-Versen et al. 2003; Tabo et al. 2005; Valluru et al. 2010), modest application of sparingly soluble rock phosphate available in the region (Hash et al. 2002), application of manure and compost (Simpson et al. 2011) and intercropping (Haynes and Mokolobate 2001). The application of lime though beneficial is limited by logistical reasons involving infrastructure, financial capacity of the smallholder farmers and transport (Rao et al. 1993; Abate et al. 2013). Since these agronomic practices differ from farmer to farmer, it is necessary to adapt breeding activities to target farmer conditions. This will also help with the problem of low adoption of improved varieties reported in WA (Ndjeunga 2002).

Breeders and farmers do not operate in a vacuum, rather within a given governmental framework. One of the main problems facing smallholder farmers is lack of affordable and accessible inputs and credit (AGRA 2014) and this boils down to governance. To be able to contribute towards sustainability of the pearl millet production systems in WA under low-P conditions, there is an urgent need for policy makers and international institutions to give primary attention to the plight of smallholder farmers in order to sustainably reduce poverty and improve food security. Governments in WA for instance need to fulfill their investment commitments under the 2003 Maputo Declaration; increase public investment in research and development activities designed to meet the challenges faced by smallholder farmers and aid in their adaptation strategies; create policy and regulatory environments that encourage private sector investments in agriculture; expedite the generation and sharing of new scientific knowledge relevant to progressive low-soil P adaptation and mitigation for example by investing in integrated soil fertility management (AGRA 2013); facilitate the breeding, testing and release of new and better-adapted, farmer-preferred crop varieties as well as improving the seed systems (AGRA 2014). Government subsidies on fertilizer are also another option for improving grain yield under low-P conditions with lessons on strengths and weaknesses for such undertakings learned from the Malawi experiences (Denning et al. 2009; Chibwana et al. 2011).

Given the looming geopolitics related to P resources, the increasing P fertilizer prices and the low purchasing power by smallholder farmers in WA, it is apparent that the low-soil P problem in pearl millet production systems in WA can only be tackled in an ‘all inclusive’ manner with stakeholders ranging right from the farmers, researchers, non-governmental organizations, international development partners and up to policy makers.

Summary

About two hundred and twenty three million people are undernourished in Sub-Saharan Africa (SSA) with 11 million people being food insecure in the Sahel region of West Africa (WA). A growing global population and climate change are expected to exacerbate this situation and present new challenges on global food production. Phosphate rock, a non-renewable resource is expected to be depleted in about 40-400 years depending on the source of information but a phosphorus (P) peak (where P demand exceeds P supply) is likely to occur before 2040. The effects of limited global P supply are expected to be felt more by resource poor smallholder farmers in SSA. This is also the region already with the lowest inorganic fertilizer use and highly weathered P deficient soils. Given these factors, breeding for low-P tolerance in crop plants offers the main environmental friendly and economically feasible strategy for improving crop productivity under low-P soils for smallholder farmers in WA conditions. This will not only contribute towards food security in the short term but also in the long term by contributing towards the efficient use of a scarce resource.

Pearl millet [*Pennisetum glaucum* (L.) R. Br.], the world’s sixth cereal crop is the hardiest of the C_4 cereals and is therefore an important food security crop in the semi-arid tropics. In the Sahel region of WA where it is the staple cereal, it contributes to food security by providing calories as well as contributing towards nutritional security by providing higher iron and zinc levels than most staple cereals. Despite this contribution towards humanity, pearl millet has received little attention in terms of research and technology and is still considered an ‘orphan’ crop. In Sahelian WA, pearl millet grows under difficult conditions of random droughts, erratic rainfall, poor soils, high temperatures and low inputs, with sometimes labor and seed being the only inputs afforded by the smallholder farmers. P has been shown to be the most limiting macronutrient on pearl millet production within this region as a result of soils with low total P, high P fixing characteristics as well as interaction with other soil micronutrient toxicities and/or deficiencies. Despite this fact, the available pearl millet germplasm had never been evaluated for grain yield performance under low-P conditions within this region prior to this study and the magnitude of the genetic component of variation had not been tested from a breeding perspective.

To fill in this knowledge gap, three genotype groups: open-pollinated varieties, inbred lines and their testcrosses were evaluated in large-scale multi-environment trials in four countries (Niger, Burkina Faso, Mali and Senegal) under two P-levels (with P fertilization and without P fertilization) between 2010 and 2012. In addition, the open-pollinated varieties and inbred lines were evaluated for P-efficiency related traits at early growth stage in pot conditions and

at mature plant stage under field conditions (inbred lines only). The main aim of these evaluations was to explore the prospects of plant breeding for improving pearl millet grain yield under low-P conditions in WA. We sought to achieve the following specific objectives: (i) to estimate quantitative-genetic parameters for grain yield in order to establish a selection strategy for pearl millet targeting P-limited environments in WA; (ii) to determine the relationship between P-efficiency related traits and grain yield in order to make inferences on which target traits should be considered in adapting pearl millet to low-P conditions in WA; and (iii) to identify genetic regions underlying quantitative traits which are related to P-efficiency based on diversity array technology (DArT) markers.

There is significant genetic variation for pearl millet performance in low-P soils; hence genetic improvement for low-P conditions should be possible. Both wide and specific adaptation can be followed in breeding pearl millet varieties for low-P conditions in WA. The decision on which adaptation method to emphasize will however depend on the clear definition of breeding objectives and the target environment for which improvement is aimed for. Direct selection of pearl millet under low-P conditions is more efficient and should be carried out in breeding activities targeting low-P environments. Landraces offer a novel genetic pool for specific adaption to low-P conditions which could be used as a valuable genetic resource for improving pearl millet. Performance under pot conditions has low genetic correlation to performance under low-P field conditions. Indirect selection under pot conditions for estimating the field performance therefore has limited applicability in pearl millet breeding activities targeting low-P field conditions. Positive mid-parent heterosis of testcrosses over inbred lines indicates potential for hybrid breeding targeting low-P environments within WA. However, given the unpredictably variable rainfall conditions under which pearl millet grows, this heterosis can only be exploited using more heterogenous hybrids like 3-way cross, double-cross or top-cross hybrids which have a substantial amount of population buffering.

Pearl millet in WA exhibits a wide genetic variation for P-uptake and internal use efficiency. Improving either of these two mechanisms in varieties targeting low-P environments is therefore feasible. P-uptake efficiency is more correlated to grain yield in pearl millet than P-utilization efficiency, and given the interactions among P, drought and other soil characteristics evident within the region, P-uptake efficiency under these conditions should be selected for. However, given the already low P content of the soils in the region and the low input conditions, genotypes selected for low-P environments should combine both P-uptake efficiency and internal P-utilization efficiency to avoid further depletion of the soils. A lower

P concentration in grain could offer a strategy for improving internal P-use efficiency in pearl millet and allow more P cycling within the farming system but there is need to properly define the effects of this on the next generation crop performance (seedling vigor), human nutrition (phytate content) and DNA composition.

Several markers showed significant association with phenotypic traits in the current study. Nine markers were associated with different P-efficiency-related traits such as P concentration in stover, P concentration in grain, P uptake and P utilization efficiency. Nine markers and thirteen markers were found to be associated with flowering time and grain yield respectively. Each of these markers individually explained between 5.5 to 15.9 % of the observed variations indicating the polygenic nature of low P tolerance in pearl millet. Some of these markers were specific to environments where they occurred (adaptive markers) whereas some were stable across environments (constitutive markers). For instance marker PgPb11603 was constitutive for early flowering whereas marker PgPb12954 was constitutive for grain yield. Several markers were also significantly associated with more than one trait for example P-uptake efficiency and grain yield implying that such traits were probably controlled by same genomic regions. The results obtained in the current study indicate potential for applying marker-assisted selection approaches in breeding activities targeting low-P environments. However further validation of these markers is necessary.

The results presented in the current study indicate potential of improving pearl millet grain yield under P-limited conditions through breeding both conventionally and through molecular technologies. However, the challenges experienced during field evaluation for low-P tolerance in the current study indicate that plant breeding alone cannot solve the effects of low-P on pearl millet grain yield. Given the global P crisis, other agronomic, socio-economic and policy approaches need to be effected alongside breeding activities if the pearl millet production system should be made sustainable to ensure food security for current and future generations.

Zusammenfassung

Ungefähr 230 millionen Menschen in Afrika südlich der Sahara (SSA) sind unterernährt; davon haben 11 Millionen Menschen in der Sahel Region von West Afrika (WA) keine gesicherte Ernährung. Die wachsende Weltbevölkerung und der Klimawandel werden diese Situation weiter verschärfen und stellen die weltweite Nahrungsmittelproduktion vor eine große Herausforderung. Man geht davon aus, dass Rohphosphat, ein nicht erneuerbarer Rohstoff, innerhalb der nächsten 40-400 Jahre aufgebraucht sein wird. Diese Angabe ist abhängig von der Informationsquelle, allerdings ist es sehr wahrscheinlich, dass eine Phosphor (P)-Knappheit (wobei die Nachfrage das Angebot übersteigt) schon vor 2040 eintreten wird. Besonders die ressourcenarmen Kleinbauern in SSA werden den Effekt von global begrenztem P-Angebot zu spüren bekommen. SSA ist die Region mit dem geringsten Einsatz von anorganischem Dünger und in der stark verwitterte Böden mit P-Mangel vorherrschen. Unter diesen Umständen bietet die Nutzpflanzenzüchtung auf P-Mangeltoleranz die umweltfreundlichste und ökonomisch sinnvollste Strategie zur Verbesserung der Produktivität für Kleinbauern in West Afrika zur verbessern. Dies wird nicht nur kurzfristig zur Ernährungssicherung, sondern auch langfristig zur effizienten Nutzung von knappen Ressourcen beitragen.

Perlhirse [*Pennisetum glaucum* (L.) R. Br.], die weltweit sechst wichtigste Getreidepflanze, ist das widerstandsfähigste C_4 Getreide und für die Ernährungssicherung in den semiariden Tropen besonders bedeutend. In der Sahelregion von WA ist es das Grundnahrungsmittel und somit entscheidend für die Ernährungssicherung sowohl als Kalorien- als auch als Nährstofflieferant, da wichtige Mikronährstoffe wie Eisen und Zink in höheren Konzentrationen vorliegen als bei anderen Getreidearten. Trotz dieses Beitrags für die Menschheit wurde Perlhirse im Hinblick auf die Forschung und Technologieentwicklung nur wenig Beachtung geschenkt und wird immer noch als ‚orphan crop‘ (verwaiste Nutzpflanze) bezeichnet. Perlhirse wächst in der Sahelregion von WA unter schwierigen Bedingungen, dazu gehören unvorhersehbare Dürreperioden, unregelmäßige Regenfälle, nährstoffarme Böden, hohe Temperaturen und geringer Eintrag an Dünger. Häufig sind der Arbeitseinsatz und das Saatgut die einzigen Mittel, die die Kleinbauern aufbringen können. Es wurde gezeigt, dass P der limitierenste Makronährstoff für die Perlhirseproduktion in dieser Region ist. Dies ist bedingt durch Böden mit geringem Gesamt P-Gehalt, hoher P-Fixierungskapazität und Wechselwirkung/Interaktion mit Giftigkeit anderer Bodenmikronährstoffe und/oder deren Mangel. Trotz dieser Tatsache wurde in WA der vorhandene Perlhirsegenpool noch nie auf

Kornertrag unter P-Mangelbedingungen erforscht. Bisher gab es noch keine Studien zur Größenordnung der genetischen Varianzkomponenten in züchterischer Hinsicht.

Um diese Wissenslücke zu schließen wurden in groß angelegten mehr-ortigen Versuchen zwischen 2010 und 2012 in vier Ländern (Niger, Burkina Faso, Mali und Senegal) die Leistung von drei Gruppen von Genotypen (offen-abblühende Sorten, Inzuchtlinien und ihre Testkreuzungen) auf Standorten mit sowie ohne P Düngung untersucht. Zusätzlich wurden die offen-abblühenden Sorten und Inzuchtlinien im frühen Wachstumsstadium unter Topfbedingungen und im Reifestadium unter Feldbedingungen (nur Inzuchtlinien) auf Merkmale, die mit P-Effizienz verknüpft sind, untersucht. Das Hauptziel dieser Untersuchungen war die Möglichkeiten der Pflanzenzüchtung zur Verbesserung des Perlhirsekornertrags unter P-Mangelbedingungen in WA zu bewerten. Die folgenden spezifischen Aufgabestellungen setzten wir uns als Ziel: (i) die Schätzung von quantitativ genetischen Parametern für Kornertrag, um eine Selektionsstrategie für Perlhirse in P-Mangelumwelten zu erstellen; (ii) Ermittlung der Beziehung zwischen Kornertrag und Merkmalen der P-Effizienz, um vorhersagen zu können, welche Zielmerkmale betrachtet werden sollten, um Perlhirse an P-Mangelbedingungen in WA anzupassen; und (iii) die Identifizierung genetischer Marker, die mit quantitativen, mit P-Effizienz in Bezug stehenden, Merkmalen korreliert sind. Dabei wurden ‚diversity array technology‘ (DArT) Marker genutzt.

Es besteht eine signifikante genetische Variation für die Leistung von Perlhirse auf Böden mit P-Mangel, sodass eine genetische Verbesserung für P-Mangelbedingungen möglich sein sollte.

Breite als auch spezifische Anpassung von Perlhirsesorten an P-Mangel können in der Züchtung angestrebt werden. Die Entscheidung, auf welche Anpassungsmethode man den Schwerpunkt legt, ist abhängig von der klaren Definition der Züchtungsziele und der betrachteten Umwelt. Eine direkte Selektion von Perlhirse unter P-Mangelbedingungen ist effizienter und sollte bei Züchtungsvorhaben für P-Mangel Umwelten bevorzugt werden. Landrassen sind spezifischer angepasst an P-Mangel als verbesserte Sorten und stellen somit eine wertvolle genetische Ressource für die Perlhirseverbesserung dar. Die genetische Korrelation der Leistungsfähigkeit unter Topf- und Feldbedingungen bei P-Mangel ist sehr gering. Indirekte Selektion unter Topfbedingungen für die Schätzung der Leistung im Feld ist somit nur begrenzt anwendbar für die Perlhirsezüchtung. Positive ‚mid-parent heterosis‘ (Heterosis relativ zum Elternmittel) der Testkreuzungen der Inzuchtlinien zeigt das Potential der Hybridzüchtung für P-Mangel Umwelten innerhalb von WA. Dennoch, angesichts der unvorhersehbaren und unregelmäßigen Regenverhältnisse unter welchen Perlhirse wächst, kann diese Heterosis nur mittels heterogener Hybriden genutzt werden. Möglich wären 3-Wege Kreuzungen, Doppel-Kreuzungen oder ‚Top-cross' Hybriden, welche ein umfangreiches Puffervermögen innerhalb der Population aufweisen. Perlhirse in WA weist eine breite genetische Variation für die Aufnahme und Nutzungseffizienz von P auf. Die Verbesserung beider Mechanismen in Sorten, die für P-Mangel angepasst werden, ist daher möglich. P-Aufnahme ist stärker mit Kornertrag korreliert als die P-Nutzungseffizienz, und in Anbetracht der Interaktion zwischen P, Dürre und anderen Bodenbedingungen in dieser Region, sollte auf P-Aufnahmeeffizienz unter diesen Bedingungen selektiert werden. Allerdings sollten bei geringem P-Gehalt des Bodens und geringem P-Eintrag Genotypen selektiert werden, die effizient in P-Aufnahme und Nutzung sind, um den Boden nicht weiter zu verarmen. Eine geringe P-Konzentration im Korn könnte eine Strategie darstellen, um die P-Nutzungseffizienz in Perlhirse zu verbessern und einen besseren P-Kreislauf innerhalb des landwirtschaftlichen Systems zu ermöglichen. Aber es besteht die Notwendigkeit den Effekt auf die Leistungsfähigkeit in der nächsten Generation (Keimfähigkeit), die menschliche Ernährung (Phytatgehalt) und den DNA-Aufbau genau zu definieren. In der vorliegenden Studie zeigten einige Marker einen signifikanten Zusammenhang mit phänotypischen Merkmalen. Neun Marker wurden mit verschiedenen Merkmalen assoziiert, die mit P-Effizienz in Verbindung stehen. Dazu gehören die P-Konzentration im Stroh, P-Konzentration in Korn, P-Aufnahme und P-Nutzungseffizienz. Eine Assoziation zwischen neun Markern und Blühzeitpunkt und dreizehn Markern und Kornertrag konnte festgestellt werden. Jeder der Marker erklärte einzeln zwischen 5,5 und 15,9 % der beobachteten Variation, was den polygenen Charakter von P-Mangeltoleranz deutlich macht. Einige der Marker waren spezifisch für die Umwelt, in der sie auftraten (‚adaptive Marker'), wobei andere über die Umwelten stabil waren (‚konstitutive Marker'). Zum Beispiel war Marker PgPb11603 konstitutiv für frühe Blüte und PgPb12954 konstitutiv für Kornertrag. Einige Marker waren mit mehr als einem Merkmal signifikant assoziiert zum Beispiel mit P-Aufnahme und Kornertrag, was bedeutet, dass diese Merkmale durch die gleiche genetische Region kontrolliert werden. Die Ergebnisse, die in dieser Studie erlangt wurden, weisen auf das Potenzial der Marker-gestützten Selektion für die Züchtung in Hinblick auf Umwelten mit P-Mangel hin. Jedoch ist eine weitere Validierung dieser Marker notwendig.

Die in dieser Studie vorgestellten Ergebnisse zeigen, welches Potential die Züchtung für die Verbesserung des Kornertrages unter P-Mangelbedingung hat, wobei die konventionelle als auch die molekulare Züchtung dienlich sind. Dennoch, Schwierigkeiten, die während der

Feldevaluierung für P-Mangeltoleranz, auftraten machen deutlich, dass Pflanzenzüchtung alleine den Effekt von P-Mangel auf den Ertrag von Perlhirse nicht lösen kann.

Angesichts der globalen P Krise ist es notwendig, dass andere agronomische, sozioökonomische und politische Ansätze neben den Züchtungsaktivitäten verfolgt werden. Nur so kann die Produktion von Perlhirse nachhaltiger und die Ernährungssicherung für die derzeitigen und nachfolgenden Generationen sichergestellt werden.

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