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Sorghum Breeding Strategies for Phosphorus-Limited Environments in Western Africa:

From Field to Genome Level

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Sorghum Breeding Strategies for Phosphorus-Limited Environments in Western Africa: From Field to Genome Level

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Content

[1]Leiser, W.L., H.F. Rattunde, H.-P. Piepho, and H.K. Parzies. 2012. Getting the Most Out of Sorghum Low-Input Field Trials in West Africa Using Spatial Adjustment. J. Agron. Crop Sci. 198: 349–359. doi:10.1111/j.1439-037X.2012.00529.x.

[2]Leiser, W.L., H.F.W. Rattunde, H.-P. Piepho, E. Weltzien, A. Diallo, A.E. Melchinger, H.K. Parzies, and B.I.G. Haussmann. 2012. Selection Strategy for Sorghum Targeting Phosphorus-limited Environments in West Africa: Analysis of Multi-environment Experiments. Crop Sci. 52: 2517–2527. doi:10.2135/cropsci2012.02.0139.

[3]Leiser, W.L., H.F.W. Rattunde, E. Weltzien, N. Cisse, M. Abdou, A. Diallo, A.O. Touré, J.V. Magalhaes, and B.I.G. Haussmann. 2014. Two in one sweep: Aluminum tolerance and grain yield in P limited soils are associated to the same genomic region in West African sorghum. BMC Plant Biology. 14: 206. doi:10.1186/s12870-014-0206-6

General Introduction

A growing world population juxtaposed with dwindling phosphorus resources presents new challenges to current and future agricultural production. The burden of depleting phosphorus resources is particularly felt in sub-Saharan Africa (SSA). The expected doubling of its population by 2050 (Cleland, 2013) and the widespread poor soil fertility (MacDonald et al., 2011) will pose an enormous task to future food security in SSA. Plant breeding can be considered as one major factor to improve agricultural production under these harsh low-input conditions. Nevertheless, until recently there have been no thorough breeding efforts to enhance crop production for low-phosphorus soil conditions in SSA.

Phosphorus - a worldwide future challenge

Phosphorus (P) is a key component of DNA, cell membranes and cellular energy, hence vital to every form of life. There is no substitute for P in food production and it is considered as the possibly most limiting mineral nutrient for plants across all arable land (Kochian, 2012). Currently, 90% of all mined rock phosphate is used in food production and its worldwide use is constantly increasing due to a higher demand in food, feed and fuel production (Cordell et al., 2009). Worldwide P reserves are expected to be exhausted in 40-400 years, depending on the source of information (Vaccari, 2009; Cooper et al., 2011; Obersteiner et al., 2013; Cordell and White, 2013) and the estimated worldwide demand for this scarce mineral (MacDonald et al., 2011; Sattari et al., 2012). Geopolitical conflicts are likely, since mineable P reserves are heavily concentrated, with Morocco holding about 75% of the global share, followed by China 6% and Algeria 3% (Jasinski, 2013). Already in 2008, P fertilizer prices were skyrocketing and have since then been on a level 2.5 times higher than in 2007. While farmers worldwide are economically affected by increasing fertilizer prices, smallholder farmers in SSA are hardest struck by such strong increases. In SSA fertilizer prices are often relatively higher than in other developing countries, mostly due to lacking infrastructure and inefficient supply chains (van der Velde et al., 2013). Already nowadays, fertilizer application rates are very low in SSA with levels mostly below 5kg P ha^{-1} (Obersteiner et al., 2013), thus leading in some regions e.g. West Africa (WA) to P deficits of the agricultural production system (MacDonald et al., 2011). Furthermore, most of the SSA soils are highly weathered low pH soils with a high P retention level (Kochian, 2012), thus fixing most (70-90%) of the applied P as plant unavailable phosphate (Holford, 1997). Therefore, there is a strong need for developing plant varieties that are more P efficient –that is, crops that produce more with less external input.

Sorghum

Sorghum (*Sorghum bicolor* L. Moench, 2n=2x=20) is the world's fifth and Africa's second most grown cereal crop (FAO, 2012). Sorghum is a staple crop of SSA and is mostly grown in resource poor regions, with the largest share in WA. Its good adaptation to harsh environmental conditions makes it an important crop for the arid and semi-arid regions, hence a crop vital for food security and increasingly for farm income in WA. Sorghum originates from northeast Africa, where most of its diversity can still be found (Henzell and Jordan, 2009). But since it is cultivated across a wide range of dryland areas across the whole world, it has several other diversity hotspots, especially in SSA (Billot et al., 2013). Cultivated sorghums (*S. bicolor ssp. bicolor*) are classified into five basic botanical races (Bicolor, Caudatum, Durra, Guinea and Kafir) and ten intermediate ones (combinations of the five basic races), based on panicle and spikelet morphology (Harlan and de Wet, 1972). Sorghum is the first fully sequenced C_4-grass and is considered a model crop for other C_4-grasses due to its relatively small (~730Mb) genome (Paterson et al., 2009).

Breeding sorghum for smallholder farmers in West Africa

Farmers in WA mostly cultivate sorghum in less fertile fields, knowing that sorghum can more dependably produce grain than can maize under such conditions. Nevertheless, limited soil P availability is a serious and frequent constraint to sorghum growth and productivity across the range of environments in WA (Buerkert et al., 2001). Although sorghum has a grain yield potential of several tons per hectare in WA, average grain yields have only been about 1t ha^{-1} since 1960 (FAO, 2012), due in part to low soil fertility and low-input production systems (Vom Brocke et al., 2010). WA sorghum is known to experience P stress below a threshold of 7-10ppm plant available soil P (Bray-1P) content (Doumbia et al., 1993). Most of smallholder farmers' fields and especially women fields show P levels below this threshold (N=207, mean=7.4, median=5.5; on-farm soil data collected by ICRISAT, Mali in 2011), therefore sorghum productivity is directly impeded by these low-P soil conditions. Increasing sorghum productivity by applying mineral P fertilizer is currently no viable option for most of the smallholder farmers in WA. The lack of financial resources, high prices, risk aversion and inadequate rural infrastructure hinder many WA farmers' use of fertilizers, resulting in average annual fertilizer application rates below 5kg P ha^{-1} (MacDonald et al., 2011; Obersteiner et al., 2013). Plant breeding is therefore a major tool to overcome this hurdle of sorghum production under smallholder farmers' conditions. Until recently there have been no broader sorghum breeding efforts to directly address these low-input production conditions. Therefore there is a strong need to develop sorghum varieties, which are better adapted to low-P cropping systems, hence serving millions of smallholder farmers and helping to assure food security in WA.

Breeding for wide versus specific adaptation

Setting up a plant breeding program for a certain target region requires prior knowledge on the climatic and edaphic conditions of this region and how they might affect variety selection. It is necessary to know which stresses (e.g. low-P soil conditions in WA) prevail in the region and how variably these stresses occur across a range of different environments within this region. Furthermore it is essential to know how different varieties react (genotype-by-environment interaction) to the various conditions in the target region. Knowledge about the prevailing stresses and the amount and type of genotype-by-environment interaction (GEI) within the target region will guide the breeder to decide how to set up a breeding program. If there is a non-cross-over type GEI with a small extend, then a breeder may choose to select for a wide genotypic adaptation across many environmental conditions within the target region. Whereas, if there is a significant rather large GEI of cross-over type, hence genotypes are differently ranked in specific environmental conditions (e.g. in low-P versus high-P conditions; Figure 1), a breeding program specifically targeting these conditions should be pursued. Likewise, genotypes with high yields and low GEI across many environments are considered as widely adapted, whereas genotypes with high yields under specific conditions and high GEI are considered as specifically adapted (Ceccarelli, 1994). Therefore, knowledge of type and extent of GEI and the specific adaptation patterns of genotypes within the target region is vital for setting up an efficient breeding program and allocating resources. Furthermore, when targeting a specific environmental condition (e.g. adaptation to low-P soils), the question arises whether direct selection under these specific conditions (e.g. low-P) or indirect selection under normal conditions (e.g. high-P) is superior. The response to direct versus indirect selection depends on the heritabilities of the target trait (e.g. grain yield) under each condition and on the genetic correlation of the target trait between both conditions (Atlin and Frey, 1989). Therefore, if genotypic performance in both conditions is highly correlated and the heritability estimates in the direct selection environment (e.g. low-P) are lower, then indirect selection would be more efficient and should be the method of choice.

Although it is widely known that P-limitation is one of the major constraints to sorghum productivity within the target region WA, there was no knowledge on the extent and type of GEI in a sorghum breeding program targeting low-P conditions, at the beginning of this study. Therefore there is a dire need to define these quantitative genetic parameters for setting up an efficient breeding strategy, which might guide sorghum breeding within WA.

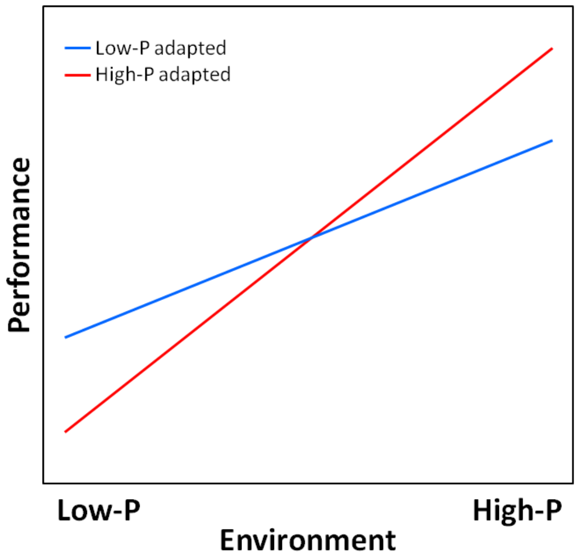

Figure 1: Genotype-by-environment cross-over interaction for low versus high P soil conditions.

Genotype selection under low-input conditions – challenges and solutions

Response to selection under low-input conditions is often considered as less efficient based on an expected lower heritability, due to an expected higher experimental error and a lower genetic variation (Ceccarelli, 1989, 1994). But contradictory results exist for this assumption (Atlin and Frey, 1989; Ceccarelli, 1994; Gallais et al., 2008; Burger et al., 2008; Mandal et al., 2010). Genetic variation has been reported to be greater in highly stressed environments, especially when locally adapted landraces were included in the trials (Ceccarelli, 1996), whereas in moderately stressed environments (cross-over point; see Figure 1) a smaller genetic variation is expected (Simmonds, 1991). Hence heritability under low input conditions can be comparable to high input conditions or even higher (Ceccarelli, 1996; Burger et al., 2008), if appropriate genetic materials are included in the study and if the experimental error is of the same magnitude as in high input conditions. The latter is mostly not the case, since spatial variation of environmental factors e.g. soil fertility, cannot be compensated by external inputs, and small fertility differences can have very large effects on plant growth especially under low-input conditions (Marschner, 1995 pp. 184–186; Voortman and Brouwer, 2003), thus genotypic variation and selection can be biased by environmental factors, leading to a higher unexplained residual variance (Grondona et al., 1996). Therefore, environmental effects need to be controlled by design and analysis for effective genotypic selection. Different field designs and corresponding analyses have been created in the last century, mostly controlling environmental heterogeneity by blocking structures and replications (Edmondson, 2005). These techniques have their limitations if spatial variation cannot be captured by the applied design. Various spatial adjustment techniques have been developed (e.g. autoregressive models) and have been shown to significantly reduce residual error, hence increase heritability and therefore make selection more efficient especially in abiotic stress environments (Gilmour et al., 1997; Singh et al., 2003). Prior to this study there was no knowledge if these methods are advantageous specifically under low-input conditions, which impact they have on genotypic selection and how they can be best employed in a breeding program targeting low-input conditions in WA.

Adaptation of plants to low-P soil conditions

Phosphorus in soils occurs mostly as orthophosphate and can be divided into mineral and organic P. More than 90% of the total soil P is inaccessible to plants since it is fixed in organic matter or as Al-, Fe- or Ca-phosphates (Mengel and Kirkby, 2001 p. 453). Plants evolved two basic adaptation strategies for soils with low plant available P levels: (1) higher P acquisition efficiency from soils and (2) improved internal physiological P use efficiency (Vance et al., 2003; Richardson et al., 2011). A higher P acquisition can be achieved by root exudates (e.g. organic anions, phosphatases), greater root biomass, changes in root architecture (e.g. root angle, root hair, aerenchyma, finer roots) and by symbioses with mycorrhiza (Lynch and Brown, 2008; Lynch, 2011; Richardson et al., 2011). A higher internal P use efficiency (e.g. more plant biomass with less P uptake) is characterized by reduced growth rate, better internal translocation, alternative respiration pathways and modified carbon cycles (Vance et al., 2003). Both adaptation strategies show a large genotypic variation in several crops. Before this study there was no knowledge on the genetic diversity of sorghum for P uptake and P use efficiency and which mechanisms might be involved.

Target traits in breeding for low-P soil conditions

Although both adaptation strategies show a large genotypic variation, most of the low-P breeding efforts have been devoted to improve P acquisition efficiency since it showed higher correlations to final grain yield production (Rose and Wissuwa, 2012). Whether P acquisition or internal P use efficiency should be considered in a breeding program depends on the soil P status and the agricultural production system targeted (Richardson et al., 2011; Simpson et al., 2011). In low-P soils with a high P retention potential, as predominant in SSA (Kochian, 2012), P acquisition efficiency is considered to be the more promising approach, whereas in high input cropping systems internal P use efficiency is regarded as more important (Wang et al., 2010). Nevertheless, both adaptation strategies should be considered in SSA in order to prevent further soil P mining (Stoorvogel et al., 1993). Most of SSA soils are characterized by low pH values, low organic matter content (C_{org}) and higher aluminum values (Al^{3+}) (Eswaran et al., 1993; Buerkert et al., 2001; Kochian et al., 2004; FAO/IIASA/ISRIC/ISS-CAS/JRC, 2012). Under these harsh conditions especially root exudates might play a major role for crop growth. Release of citrate and other organic anions into the rhizosphere prevents root damage by chelating Al^{3+} and can lead to more plant available P by mobilizing previously bound P mainly by ligand exchange, dissolution and occupation of P sorption sites (Zhang et al., 1997; Neumann and Römheld, 1999; Ma et al., 2001). Thus, exudation of organic anions can lead to a higher P acquisition rate by releasing more bound P and keeping roots intact for further soil exploration (Richardson et al., 2011). Plant growth under such stressful conditions as prevalent in WA, is not merely restricted to a sole abiotic or biotic stressor (Haussmann et al., 2012). Considering these other constraints (e.g. foliar and root diseases, other minerals and water stagnation or drought) in a breeding program targeting low-P conditions can lead to big yield increases under low-P conditions, without actually targeting traits directly related to higher P acquisition or internal P use efficiency (Simpson et al., 2011). Therefore, breeding crops adapted to low-P soil conditions is a complex task and must be seen as one tool among other measures to close the yield gaps in SSA (Mueller et al., 2012) and make the whole agricultural production system more nutrient efficient and sustainable. Before this study there was no knowledge on which adaptation strategy is the more important one contributing to the adaptation of WA sorghum to low-P soil conditions. Furthermore it is not known which P-efficiency trait should be considered as selection criteria for grain yield selection under low-P conditions and how different criteria can be combined.

Genetics of low-P adaptation and its possible use in sorghum

The underlying genetics of low-P adaptation have extensively been studied in *A. thaliana* (for review see: Nilsson et al., 2010; Rouached et al., 2010; Hammond and White, 2011) revealing a complex adaptation and response network. Nevertheless, most of these genes could not lead to higher yields in crop plants under field conditions. Among crop plants, rice is the most extensively studied one (Lafitte et al., 2007; Shimizu et al., 2008; Chin et al., 2009, 2011; Panigrahy et al., 2009; Torabi et al., 2009; Li et al., 2009, 2010; Secco et al., 2010; Park et al., 2010; Famoso et al., 2011; Gamuyao et al., 2012; Topp et al., 2013). The most important quantitative trait locus *PUP-1*, which was shown to increase grain yield under low-P field conditions, was first mapped in 1998 (Wissuwa et al., 1998). Underlying *PUP-1* is a single kinase gene, *PSTOL1*, which increases early root growth and P acquisition efficiency under low-P conditions and in several different genetic backgrounds (Gamuyao et al., 2012). *PSTOL1* is one of the few genes, which was proven to contribute to enhanced productivity under low-P field conditions and is not merely a scientific concept. Since the rice genome exhibits substantial synteny to other grasses including sorghum (Soderlund et al., 2006; Ramu et al., 2009), it might be possible to exploit the genetic knowledge from rice and find similar genes to *PSTOL1* in sorghum, which contribute to better root growth and higher P uptake rates under low-P conditions. Before this study there was no knowledge about the effect of several candidate genes, related to P efficiency, on the adaptation of sorghum to low-P soil conditions.

Genome wide association studies

Genome wide association studies (GWAS), also known as linkage disequilibrium (LD) mapping, is a well established method to decipher the underlying genetic structure of simple or complex traits by exploiting the LD between DNA markers and the underlying causative genes of a specific trait, which is present in a germplasm set. It has been widely used in human and plant genetics (Hirschhorn et al., 2002; Zhu et al., 2008) and overcomes certain limitations of the classical linkage analysis mapping in plants, such as a restricted allelic diversity and a limited genomic resolution (Zhu et al., 2008; Brachi et al., 2011). In combination with new DNA sequencing technologies e.g. genotyping-by-sequencing (Elshire et al., 2011), the mapping resolution and thus the chance of detecting causative SNPs using GWAS increased immensely (Morris et al., 2013). Employing GWAS using high resolution markers in a diverse set of sorghum genotypes, makes it possible to examine the genetics underlying the adaptation of sorghum to low-P soil conditions. No such study has been conducted before this study.

Objectives of this study

The goal of my thesis was to establish a selection strategy for breeding sorghum targeting P- limited soils in WA. In particular the following specific objectives were:

1. To evaluate the impact of spatial models on genotypic selection in low-input field trials.
2. To develop a selection strategy for sorghum targeting P-limited environments based on quantitative genetic parameters.
3. To identify genomic regions influencing sorghum performance in P-limited environments using modern genomic tools.

Getting the most out of sorghum low-input field trials in West Africa using spatial adjustment[1]

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The original publication is available at: http://onlinelibrary.wiley.com/doi/10.1111/j.1439-037X.2012.00529.x/full

Abstract

Breeding sorghum for low-input conditions is hindered by soil heterogeneity. Spatial adjustment using mixed models can help account for this variation and increase precision of low-input field trials. Large small-scale spatial variation (CV 39.4%) for plant available phosphorous was mapped in an intensely sampled low-input field. Spatial adjustments were shown to account for residual yield differences due to this and other growth factors. To investigate the potential of such models to increase the efficiency of low- and high-input field trials, 17 experiments with 70 sorghum genotypes conducted in Mali, West Africa, were analyzed for grain yield using different mixed models including models with autoregressive spatial correlation terms. Spatial models (AR1, AR2) improved broad sense heritability estimates for grain yield, averaging gains of 10 and 6 percentage points relative to RCB and lattice models, respectively. The heritability estimate gains were even higher under low-P conditions and in two-replicate analyses. No specific model was best for all environments. A single spatial model, AR1xAR1, captured most of the gains for heritability and relative efficiency provided by the best model identified for each environment using Akaike's Information Criterion. Spatial modeling resulted in important changes in genotype ranking for grain yield. Thus, the use of spatial models was shown to have potentially important consequences for aiding effective sorghum selection in West Africa, particularly under low-input conditions and for trials with fewer replications. Thus, using spatial models can improve the resource allocation of a breeding program. Furthermore, our results show that good experimental design with optimal placement and orientation of blocks is essential for efficient statistical analysis with or without spatial adjustment.

[1]Leiser, W.L., H.F. Rattunde, H.-P. Piepho, and H.K. Parzies. 2012. Getting the Most Out of Sorghum Low-Input Field Trials in West Africa Using Spatial Adjustment. J. Agron. Crop Sci. 198: 349–359. doi:10.1111/j.1439-037X.2012.00529.x.

Selection Strategy for Sorghum Targeting Phosphorus Limited Environments in West Africa: Analysis of Multi-Environment Experiments[2]

Willmar L. Leiser, H. Frederick W. Rattunde, Hans-Peter Piepho, Eva Weltzien, Abdoulaye Diallo, Albrecht E. Melchinger, Heiko K. Parzies, Bettina I.G. Haussmann

The original publication is available at: https://www.crops.org/publications/cs/articles/52/6/2517

Abstract

Although sorghum [*Sorghum bicolor* (L.) Moench] in West Africa (WA) is generally cultivated with limited or no fertilization on soils of low phosphorous availability, no assessments of the genetic variation among WA sorghum varieties for adaptation to low soil P are known. We assessed grain yields of 70 diverse sorghum genotypes under –P (no P fertilization) and +P conditions at two locations in Mali over five years. Genetic variation for grain yield under –P conditions and the feasibility and necessity of sorghum varietal testing for grain yield under –P conditions were evaluated. Delayed heading dates (0-9.8 d) and reductions of grain yield (2-59%) and plant height (13-107cm) were observed in –P relative to the +P trials. High estimates of genetic variance and broad sense heritabilities were found for grain yield across both –P (h^2=0.93) and +P (h^2=0.92) environments. The genetic correlation for grain yield performance between –P and +P conditions was high (r_G=0.89), suggesting that WA sorghum varieties generally possess good adaptation to low P conditions. However, genotype x phosphorus crossover interaction was observed between some of the highest yielding genotypes from the –P and +P selected sets, with the variety IS 15401 showing specific adaptation to –P. Direct selection for grain yield in –P conditions was predicted to be 12% more efficient than indirect selection in +P conditions. Thus, selection under –P conditions should be useful for sorghum improvement in WA.

[2]Leiser, W.L., H.F.W. Rattunde, H.-P. Piepho, E. Weltzien, A. Diallo, A.E. Melchinger, H.K. Parzies, and B.I.G. Haussmann. 2012. Selection Strategy for Sorghum Targeting Phosphorus-limited Environments in West Africa: Analysis of Multi-environment Experiments. Crop Sci. 52: 2517–2527. doi:10.2135/cropsci2012.02.0139.

Two in one sweep: Aluminum tolerance and grain yield in P-limited soils are associated to the same genomic region in West African Sorghum[3]

Willmar L. Leiser, Henry Frederick W. Rattunde, Eva Weltzien, Ndiaga Cisse, Magagi Abdou, Abdoulaye Diallo, Abocar O. Tourè, Jurandir V. Magalhaes, Bettina I.G. Haussmann

The original publication is available at: http://www.biomedcentral.com/1471-2229/14/206/

Abstract

Background

Sorghum (*Sorghum bicolor* L. Moench) productivity is severely impeded by low phosphorus (P) and aluminum (Al) toxic soils in sub-Saharan Africa and especially West Africa (WA). Improving productivity of this staple crop under these harsh conditions is crucial to improve food security and farmer's incomes in WA.

Results

This is the first study to examine the genetics underlying sorghum adaptation to phosphorus limitation in a wide range of WA growing conditions. A set of 187 diverse sorghum genotypes were grown in 29 –P and +P field experiments from 2006-2012 in three WA countries. Sorghum grain yield performance under –P and +P conditions was highly correlated (r=0.85***). Significant genotype-by-phosphorus interaction was detected but with small magnitude compared to the genotype variance component. We observed high genetic diversity within our panel, with rapid linkage disequilibrium decay, confirming recent sequence based studies in sorghum. Using genome wide association mapping based on 220 934 SNPs we identified one genomic region on chromosome 3 that was highly associated to grain yield production. A major Al-tolerance gene in sorghum, *SbMATE*, was collocated in this region and *SbMATE* specific SNPs showed very high

[3]Leiser, W.L., H.F.W. Rattunde, E. Weltzien, N. Cisse, M. Abdou, A. Diallo, A.O. Touré, J.V. Magalhaes, and B.I.G. Haussmann. 2014. Two in one sweep: Aluminum tolerance and grain yield in P limited soils are associated to the same genomic region in West African sorghum. BMC Plant Biology. 14: 206. doi:10.1186/s12870-014-0206-6

associations to grain yield production, especially under –P conditions, explaining up to 16% of the genotypic variance.

Conclusion

The results suggest that *SbMATE* has a possible pleiotropic role in providing tolerance to two of the most serious abiotic stresses for sorghum in WA, Al toxicity and P deficiency. The identified SNPs can help accelerate breeding for increased sorghum productivity under unfavorable soil conditions and contribute to assuring food security in WA.

General Discussion

Spatial adjustments – applications and implications in low-P breeding

Genotype selection in low-input and stress prone field trials is generally hampered by environmental noise, which cannot be accounted for by standard analysis of field trials. Consequently these trials can show lower broad-sense heritability (h^2) within and across environments (Weber et al., 2012), hence leading to a lower response to selection. Although additional measures e.g. soil/plant parameters, can lead to an increased h^2 by using them as covariates in a standard analysis (Mühleisen et al., 2013), particularly soil parameters account mostly only for a small proportion of genotypic performance (Voortman and Brouwer, 2003; Leiser et al., 2012a), are laborious to collect and expensive to analyze. Hence, spatial adjustment methods accounting for any environmental variation are a suitable inexpensive way of correcting for micro-variability and should be considered especially in trials, where spatial variability is due to many not clearly identifiable factors, such as in most of the soils in WA (Brouwer et al., 1993). In the present field trials, spatial trends were mostly identified along rows and columns, leading to the selection of spatial models accounting for both trends (Leiser et al., 2012a). These findings led us at ICRISAT-Mali to the conclusion to lay out our incomplete blocks in two-dimensions comprising both rows and columns in current field trials. This practice led generally to similar high h^2 estimates using either incomplete block or spatial model analyses (data not shown), thus showing that proper blocking based on prior knowledge can replace spatial adjustment methods as already proposed in Leiser et al. (2012a). Since two-dimensional blocking is incorporated in the R package DiGGer (www.austatgen.org), it can be easily applied in any breeding program, without the need to invest money into expensive software which can model spatial covariance structures in a mixed model framework.

Whichever approach is finally chosen, in low-P field trials it is essential to correct properly for external errors either by design and/or analysis. It was shown that the use of spatial models, especially under low-P conditions, will lead to significantly higher h^2 estimates, more precise genotype estimates and different genotypic rankings, hence influencing genotype selection (Leiser et al., 2012a; b). In the era of molecular breeding, using either QTL-based or genomic selection methods, good phenotypic data are essential to identify marker-trait associations. The power of detecting QTLs (Riedelsheimer et al., 2012a) and the accuracy of genomic prediction (Lado et al., 2013) are increasing with increasing h^2, hence spatial models, which can lead to more precise phenotypic data, are of great importance also for molecular breeding efforts targeting stress prone environments. The evaluated low-P trials can be considered as highly stress-prone environments, with large reductions of grain yield and plant height and delayed heading (Leiser et al., 2012b). Therefore, applying proper field designs and/or spatial modeling was a necessary step to gain phenotypic data, which could be used to formulate a sound breeding strategy and find genomic regions for future sorghum breeding targeting low-P soil conditions in WA.

Genotypic variation and selection of sorghum for adaptation to low-P soils

Sorghum growth is severely impeded under P deficient conditions. It shows large grain yield and plant height reductions and delay of flowering as observed in several plants (Rossiter, 1978; Fageria et al., 1988; Atlin and Frey, 1989; Wissuwa and Ae, 2001; Manske et al., 2001; Turk et al., 2003; Chen et al., 2008; Cichy et al., 2008; Parentoni et al., 2010; Leiser et al., 2012b). Nevertheless, sorghum germplasm from WA is generally better adapted to low-P soils compared to other crops as seen in a stronger relationship between performance under high-P and low-P conditions (Atlin and Frey, 1989; Beebe et al., 1997; Hammond et al., 2009; Parentoni et al., 2010; Ding et al., 2012; Leiser et al., 2012b). However, there is great genetic variation for response to P fertility status, with some genotypes showing significantly superior grain yields only under low-P conditions, hence giving the opportunity for selection for specific adaptation to soil P fertility status. A significant genotype-by-P cross-over type interaction, particularly among the best performing genotypes and similar high broad-sense heritabilities in low and high-P conditions, led to a higher response of direct selection under low-P conditions relative to indirect selection under high-P conditions (Leiser et al., 2012b) and points to the need of directly selecting sorghum under low-P conditions (<7 ppm Bray-1 P) to meet the needs of millions of smallholder farmers in WA, which generally crop sorghum under low-input conditions with plant available soil P levels below 7ppm.

The evaluated set of genotypes in this study represented a wide range of sorghum diversity originating from WA. Although there were generally significant genotypic differences for low-P adaptation, some genotype groups showed distinct patterns. Among the racial groups, particularly genotypes of the Guinea and Durra race showed specific adaptation to low-P conditions, whereas the Caudatum-race genotypes were more adapted to high-P conditions (Leiser et al., 2014a; b). In WA, Guinea sorghums are mostly cultivated in the more wet Sudanian zone, whereas Durra sorghums are predominantly cultivated in the rather dry Sahelian zone (Zongo et al., 1993; Deu et al., 2008; Sagnard et al., 2011). Hence, these two races are promising germplasm pools for sorghum breeding targeting P-limited conditions in different agroclimatic and farmer preferential zones in WA. Furthermore, genotypes classified as landraces were more specifically adapted to low-P conditions than varieties originating from breeding programs. This may reflect the selection history of both germplasm groups, while landraces have been selected by farmers under low-P conditions for millennia; official sorghum breeding was mostly conducted under well fertilized conditions. But since both variety types showed significant within group variation for grain yield under low-P conditions, both of them can be exploited to enhance grain yield production under farmer's field's conditions.

The projected climate with more variable on- and off-sets of the rainy season will pose another great challenge to sorghum production in WA. Photoperiod sensitivity of sorghum is proposed to be a crucial property to better cope with these more variable rainfall events (Dingkuhn et al., 2006; Haussmann et al., 2012). Photoperiod sensitive genotypes proved to be more specifically adapted to low-P conditions, showed less delay in heading and had a higher P uptake rate than photoperiod insensitive varieties (Leiser et al., 2014b). It was observed that whereas photoperiod-insensitive sorghums having linear growth, early sown photoperiod sensitive sorghums exhibit bilinear rates of above ground growth (Clerget et al., 2008) whereas rooting depth continues at a constant rate, suggesting that P uptake rates can be maintained at later growth stages. Similar findings on phenological delay, root growth duration and adaptation to low-P conditions were also observed in *A. thaliana* (Nord and Lynch, 2008), pointing to the need of further research on this adaptation mechanism. By and large, photoperiod-sensitive sorghum genotypes provide a valuable germplasm source for future breeding efforts targeting low-P soil conditions and more variable rainy seasons in WA.

WA sorghum exhibits a large genetic variation for P uptake and P utilization traits and proves to use P more efficiently than maize (Parentoni and Souza Jr., 2008; Leiser et al., 2014b). To date no single mechanism for the observed higher P uptake level of some genotypes is known. We, at ICRISAT-Mali, evaluated all 187 sorghum genotypes under low-P soil conditions (<6ppm Bray-1 P) in a pot experiment for 38 days and measured mycorrhiza colonized root length and crown root angle, two major factors generally influencing P uptake in plants (Richardson et al., 2011). Mycorrhiza colonization had a negative influence on biomass production and P uptake at an early developmental stage, probably reflecting „carbohydrate costs“ of initial mycorrhizza colonization (Olatoye, 2013), and neither of the traits was correlated to grain yield production across 15 independent low-P field trials. This suggests that several different mechanism are involved in P acquisition of sorghum (unpublished data). Hence further research is needed to understand the possible mechanisms and how they interact and complement each other in different types of environments. Such knowledge could further guide breeders for specifically enhancing P acquisition efficiency in sorghum.

Although P uptake traits are generally better at predicting grain yield across low-P conditions than P use efficiency traits (Jones et al., 1989; Manske et al., 2001; Araújo and Teixeira, 2003; Ozturk et al., 2005; Cichy et al., 2008; Parentoni et al., 2010; Leiser et al., 2014b), selection for a higher P use efficiency should be considered especially in breeding programs targeting areas that show P deficits of the overall agricultural production system and where high P uptake would lead to further soil P depletion (MacDonald et al., 2011; Rose and Wissuwa, 2012; van der Velde et al., 2014). The observed genetic variation for P use efficiency in WA sorghum and its positive correlation to grain yield production allow genotypic selection for a higher P use efficiency without any negative impact on final grain yield production in P-limited conditions (Leiser et al., 2014b). Leiser et al. (2014b) showed that P concentration in the grain is a reliable, simple and rather inexpensive measure of P use efficiency, which meets the criteria of being not confounded by harvest index (Rose et al., 2011; Rose and Wissuwa, 2012). Hence selection for a lower P concentration in the grain might be pursued to enhance P use efficiency, thus contributing to minimize further soil P mining in WA. The likely concurrent reduction of phytic acid content in the grain could increase Zn and Fe bio-availability (Hurrell et al., 2003), which would be of great importance in WA where most of the grain is used for food and a high level of malnutrition is still prevailing (Birner et al., 2007), but it might also lead to less vigorous early plant growth, hence has a negative impact on final biomass production under low-P conditions (Veneklaas et al., 2012). Moreover, a high P acquisition rate is also crucial for grain yield production in soils with a high P retention potential, as commonly occurring in WA (Kochian, 2012). Since genotypes were indentified combining a high P acquisition and high P use efficiency, leading to superior grain yield performance under low-P conditions, it was shown that both traits can be combined in one genotype. Exploiting natural variation is therefore a promising tool for enhancing overall P efficiency (Lynch, 2007).

Genetics underlying adaptation to low-P conditions in sorghum

Although sorghum is extensively cultivated under low-P conditions and its genome has been fully sequenced and has been available since 2009 (Paterson et al., 2009), no study ever looked comprehensively at the genetic variation and the underlying genetics of low-P adaptation in sorghum. Due to its African origin (Wet and Harlan, 1971) and its long cultivation in WA under P-limited conditions, WA sorghum provides a promising source for studying the genetic architecture of several traits related to low-P adaptation.

Two approaches were followed for examining the genetics underlying low-P adaptation in sorghum. First, SNPs within candidate gene homologs from *A. thaliana* and rice were identified and associated to low-P performance and secondly a whole genome scan using 220,934 SNPs derived from genotyping-by-sequencing (Elshire et al., 2011) was conducted. Although many SNPs were identified and studied in several different genes (namely homologs of: *OsPHR2*, *SIZ1*, *PHO2*, *OsSPX1*, *PHT1*, *PSTOL1*) involved in P starvation response, with functions ranging from P transporter, transcription factor, mycorrhiza inducer, root growth and P signaling (Fang et al., 2009; Nilsson et al., 2010; Rouached et al., 2010b; Gamuyao et al., 2012), no strong associations to traits related to low-P adaptation were identified, except for *PSTOL1* homologs. *PSTOL1* is the underlying gene of a major P uptake QTL (*Pup-1*) in rice. It encodes a protein kinase and enhances early root growth and P uptake under low-P conditions (Gamuyao et al., 2012). SNPs within two *PSTOL1* homologs located on chromosome 3 and 7, showed significant associations to early shoot P uptake and shoot biomass production, and to grain yield under low-P conditions in the evaluated WA sorghum diversity panel. The same SNPs were also associated to grain yield and P uptake under low-P field conditions and to several root architectural traits in nutrient solution in a genetically independent mapping population evaluated in Brazil (Hufnagel et al., 2014). These results indicate that *PSTOL1* homologs in sorghum have the ability to stably enhance P uptake and crop performance under low-P soil conditions by a mechanism related to early root growth enhancement, similar to *PSTOL1* in rice (Gamuyao et al., 2012). Although significant associations of the *PSTOL1* homologs to grain yield production under low-P field conditions were found, they generally only explained a small proportion (r^2<7%) of the genotypic variance.

Using 220,934 SNPs in a genome wide association study, one specific region was identified, which was highly associated to grain yield production under P-limited conditions. The Al-tolerance locus Alt_{SB} and its underlying gene *SbMATE* in sorghum was collocated in this region and Alt_{SB} specific SNPs showed very high associations to grain yield production, especially under low-P conditions, explaining up to 16% of the genotypic variance. The results suggest that Alt_{SB} has a pleiotropic role in providing tolerance to two of the most serious abiotic stresses for sorghum in WA, Al toxicity and P deficiency. Previously it was suggested that Al-tolerance and P uptake under low-P conditions can be regulated by similar processes in sorghum, since Alt_{SB} was associated to a higher citrate release of sorghum roots (Magalhaes et al., 2007). Release of citrate and other organic anions into the rhizosphere prevents root damage caused by Al-toxicity by chelating Al^{3+}. At the same time, citrate can mobilize P that is bound to soil clays by ligand exchange, dissolution and occupation of sorption sites, thus increasing P availability to the plants (Zhang et al., 1997; Neumann and Römheld, 1999; Ma et al., 2001). Hence, exudation of organic anions can lead to a higher P acquisition rate (Vance et al., 2003; Richardson et al., 2011). Recent work showed that over-expression of citrate synthesis and malate transporter genes in different species resulted in improved Al-tolerance and enhanced P uptake under low-P conditions (Delhaize et al., 2009; Wang et al., 2013; Liang et al., 2013), supporting previous hypotheses that Al-tolerance and P uptake can be regulated by similar mechanisms (Magalhaes et al., 2007). The presented findings can be regarded as a further step to prove these assumptions under field conditions. Although the frequency of the positive low-P specific and Al-tolerant SNPs was low (9%) in the evaluated WA sorghum panel, the frequency is much higher in the Guinea-race germplasm, with 95% of the genotypes carrying the positive *SbMATE* alleles being either pure Guinea race or Guinea introgressed genotypes. A similar allele frequency of these SNPs and a higher frequency in WA Guinea sorghums was also found in a worldwide sorghum collection (Caniato et al., 2011), hence pointing to this germplasm group as an important source for Al-tolerance in sorghum (Caniato et al., 2014). Since both, P-limitation and Al-toxicity show a great spatial variation (Voortman et al., 2004) and have been reported to have a major influence on crop growth in WA (Manu et al., 1996), marker assisted selection targeting both traits simultaneously, can and should be carried out to achieve genotypes with a staple performance across multiple soil conditions in WA.

Although a highly associated genomic region with a plausible molecular link to low-P adaptation was identified, only a small proportion (r^2<20%) of the total genotypic variance could be explained by this region (Leiser et al., 2014a) and no single adaptation strategy (e.g. P uptake, P use efficiency) could be identified (Leiser et al., 2014b). Hence adaptation of sorghum to P-limited soils is a complex, highly polygenic trait, encompassing different adaptation strategies involving P acquisition and or internal P use efficiency. A method of choice to overcome these hurdles of complexity may be genomic selection. In contrast to QTL-based selection strategies, genomic selection does not involve significance tests and uses all available markers to predict genotypic performance (Meuwissen et al., 2001), hence minor QTLs will not be neglected in genotypic selection. It gained recently much more attention in plant breeding, especially for highly polygenic traits, due to its higher response to selection compared to QTL-based or phenotypic selection (Heffner et al., 2010; Jannink et al., 2010; Massman et al., 2012). To exploit the potential of genomic selection for adaptation to P-limited environments, the predictive ability of genomic selection within our diversity set was estimated for grain yield under low-P, high-P, across both low and high-P conditions and for grain yield ratios, as a measure for low-P specificity (Figure 2). Due to its generally good robustness and performance (Riedelsheimer et al., 2012b; Wimmer et al., 2013), the RR-BLUP-method was applied, as implemented in the R package rrBLUP (Endelman, 2011). Fivefold cross-validation with 100 replications was used to assess the prediction performance in our diversity panel. The data set was divided into five mutually exclusive subsets; four of them formed the training set for fitting marker effects and the fifth subset was used as a validation set. Its genotypic values were estimated using the formerly estimated marker effects of the training set (Endelman, 2011). Pearson's correlation coefficient between predicted genotypic values and observed phenotypic values in the validation set describes the predictive ability. A high predictive ability could be found for grain yield under low-P, high-P and across both fertility conditions and a moderate one for grain yield ratios (Figure 2). These findings suggest that a higher response to selection can be reached by using genome wide approaches compared to QTL-based or phenotypic selection (Massman et al., 2012). Nevertheless, since Al-toxicity is a widespread production constraint with a high spatial variability across WA, it is necessary to specifically consider this trait in a selection program targeting a wide range of edaphic conditions. Due to its mostly monogenic inheritance pattern (Caniato et al., 2014) and its low frequency in WA sorghum breeding material (Leiser et al., 2014a), it would be necessary to use an altered selection scheme. One possible option would be first to employ a single marker selection for the positive Alt_{SB} alleles (Caniato et al., 2014) and then apply a consecutive genomic selection step to further select the potentially best performing progenies among the Al-tolerant progenies. Another option would be to use prediction methods e.g. BayesB, LASSO, which might give more weight to specific QTLs in a genome wide selection approach (Daetwyler et al., 2010; de los Campos et al., 2013; Wimmer et al., 2013). Which genome wide approach will be chosen depends on the costs of DNA extraction and marker analyses. To date, the approach with prior Al-tolerance selection, is the more cost efficient one, hence is the method of choice to simultaneously increase Alt_{SB} allele frequency and improve overall grain yield performance in WA sorghum.

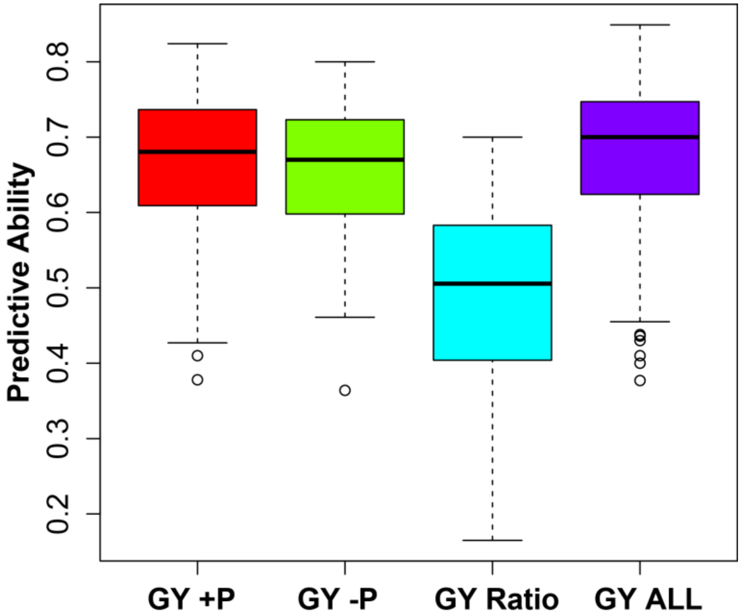

Figure 2: Genomic selection predictive ability of grain yield BLUPs across +P, -P sites separately and combined (GY ALL) and grain yield ratios as –P/+P performance. Values derived from 5-fold cross-validation with 100 replications using RR-BLUP.

Conclusions and implications for applied sorghum breeding in West Africa

Sorghum breeding efforts targeting P-limited environments in WA were already initiated in 2006 at ICRISAT-Mali. Nevertheless, only with the presented findings in this study the necessity and possibility of breeding sorghum for low-P soil conditions in WA was clearly laid out. The following conclusions can be drawn, which are of direct relevance for sorghum breeding targeting P-limited environments in WA:

- Adequate field designs and/or spatial analyses are necessary tools for efficient genotype selection under low-input conditions
- WA sorghum is generally well adapted to low-P soil conditions and shows a large exploitable genetic variation for P efficiency
- Direct selection under low-P conditions is feasible, necessary and more efficient than indirect selection under high-P conditions.

- Landrace genotypes are more specifically adapted to low-P conditions and show a higher P acquisition capacity than researcher bred varieties
- Durra and Guinea race sorghums are a very promising source germplasm with a high low-P specificity
- Photoperiod sensitive genotypes show less delay in heading, a higher P acquisition rate and low-P specificity, hence providing a valuable germplasm source for climate and low-P resilience breeding
- Selection for low P concentration of grain can be used to enhance internal P use efficiency, without any negative impact on grain yield production
- SNPs in PSTOL1 homologs of rice stably enhance P uptake and crop performance of sorghum under low-P soil conditions and can be used in marker assisted selection to increase root growth and final grain yield production
- P-efficiency and Al-tolerance are pleiotropically regulated by the same genomic region. SNPs of this region can be used for marker assisted selection.
- WA Guinea race sorghum is a major source for Al-tolerant and low-P specific SNPs and can serve as source germplasm for allele mining and marker assisted selection
- Genomic selection appears to be a very promising approach to further increase the response to selection. Methods giving more weight to single SNPs should be considered

Future Challenges

The presented findings show that breeding sorghum for P-limited soils is necessary and possible using different approaches. Although the presented conclusions were based upon a very good dataset, there are still many open questions and new challenges arising, which need to be addressed to increase sorghum production not just across a few sites, but on a large scale across millions of smallholder farmer's fields in WA. First of all, I will present breeding challenges which are directly arising from the presented work and can and partly will be addressed in the near future. Afterwards, I will raise some issues, which are not directly related to breeding research, but are of major agronomic and socio-economic importance, and must be considered to tackle the issue of food and P scarcity in WA in an integrated manner.

Breeding challenges

The identified SNP markers for grain yield production under low-P conditions will need to be further validated to draw final conclusions and give final advices on how to proceed. At ICRISAT-Mali, we are currently evaluating further large diversity (571 genotypes) and bi-parental mapping sets (14 bi-parental populations, each having approx. 100 genotypes) for performance under low and high-P conditions to validate these SNPs. Furthermore, expression or knock-out studies of the identified genes will be necessary to prove the postulated mechanisms. Once validated, it should be possible to incorporate the desired loci for both traits into elite breeding material with minimum linkage drag using marker assisted selection. Furthermore, the already validated gene specific markers for Al-tolerance will make allele mining possible in large germplasm collections, hence increase allelic frequency and Al-tolerance of the currently used germplasm in WA. These markers have been converted to the cost-efficient (0.08€/data point) KASP system of LG Genomics and are available on the Integrated Breeding Platform of the Generation Challenge Programme (https://www.integratedbreeding.net/), hence can be directly used by all breeders in WA. Once validation steps are completed all other markers will be converted to the KASP-system and made accessible on the same open breeding platform.

I could show that genomic selection provides a promising tool for grain yield selection. Nevertheless, the presented data were derived *in-silico* using cross validations. Therefore further validation steps with an independent set of genotypes will be required to prove the effectiveness of genome wide versus QTL-based selection. At ICRISAT-Mali, we are currently evaluating 571 S1-progenies derived from a random mating population, comprised of 13 genotypes of which 12 were part of our diversity panel. The derived S1-lines are currently genotyped for the identified SNPs and using GBS. This will give us the option to compare genome wide and QTL-based selection approaches, with a somewhat independent set of genotypes in independent environments. Once validated, all GBS marker effects will be made publicly available and can be used to predict genotype performance in other breeding populations in WA.

Several adaptation mechanisms are involved in low-P adaptation. We could not detect a single mechanism which can be considered as major determinant for grain yield production under low-P conditions. Since we used a very diverse panel of sorghum genotypes, several mechanisms and strategies might have been involved in P adaptation. Using a less diverse set or even a bi-parental mapping population derived from contrasting genotypes might be an option to detect single contributing mechanisms. At ICRISAT-Mali there are several bi-parental populations available, which could be suitable for such a study. Especially populations having IS15401 as one parent should be a valuable source for such studies. IS15401 proved to be the most specific low-P adapted genotype, which showed a high P-use efficiency, high Al-tolerance, carrying Alt_{SB}, *Striga hermonthica* resistance, midge resistance, high photoperiod sensitivity and high grain yields under low-P conditions.

Sorghum hybrid breeding is currently gaining much momentum especially in Mali. The lately released hybrid cultivars show farmer-preferred characteristics and yield superiorities of approximately 30% across multiple on-farm conditions compared to commonly used line cultivars (Rattunde et al., 2013). A steadily increasing seed demand (25t in 2012, 50t in 2013) for hybrid seed in Mali shows the importance of hybrid sorghum breeding for WA. To date there is no profound knowledge on the design of a hybrid sorghum breeding program specifically targeting low-P conditions. ICRISAT-Mali in collaboration with the University of Hohenheim will address this issue in a follow-up project from 2014-2017 ("Bringing the benefits of heterosis to smallholder sorghum and pearl millet farmers in West Africa").

Agronomic and socio-economic challenges

Breeding crops for higher yields under low-input conditions is a very promising tool to enhance food production in WA. Nevertheless, plant breeding must be considered in the context of the entire agricultural production system, hence it plays only one part in tackling food and soil nutrient scarcity in WA. Agronomic and socio-economic measures have vital roles in sustainable and P efficient production systems and for adoption of newly developed technologies (Cordell and White, 2013).

Due to infrastructural and financial constraints of many smallholder farmers, a broad and highly intensified mineral fertilizer application is currently no valid option in WA. Agronomic measures such as intercropping (Henry et al., 2008), crop rotations (Horst et al., 2001), livestock integration, manure and compost applications (Simpson et al., 2011) display production measures, which are less dependable on external inputs and therefore provide options to smallholder farmers, which are most affected by low soil fertility conditions. Although the mentioned agronomic measures can help enhance crop production under P-limited conditions, their usefulness to improve Al-tolerance or decrease Al-toxicity is rather limited. It was shown that Al-toxicity and P-deficiency can be reduced by incorporating crop residues, hence increasing soil organic matter (Haynes and Mokolobate, 2001), nevertheless, applying lime ($CaCO_3$) is generally the method of choice to ameliorate soils, which show high levels of Al-toxicity (Pavan et al., 1984; Moody et al., 1998; Ila'ava et al., 2000). To date liming is no viable option to smallholder farmers in WA, due to the lack of and access to lime. Therefore the only sustainable solution for WA is to increase soil organic matter through agronomic measures and improve Al-tolerance within the current breeding germplasm. Since P efficiency and Al-tolerance are associated to the same genomic region and are most likely pleiotropically regulated by *SbMATE*, genotypic selection for Al-tolerance will also have a positive impact on P efficiency in WA sorghum, hence plant breeding provides a very important tool amongst other options to enhance crop production in WA.

In recent decades several methods have been developed and proven to be effective in enhancing crop production under low-input conditions and many high yielding sorghum varieties have been released in WA. Nevertheless, the adoption rates of these new tools have been limited on farm level. Many factors were identified for being responsible for the observed lack of adoption among farmers, ranging from political and socio-economic to agronomic reasons (CGIAR and Stoop, 2002). By proper identification of the farmers' needs using participatory research methodologies (e.g. participatory plant breeding), on-farm validation and farmer-led testing of new technologies under minimal risk (e.g. seed mini-packs), strengthening of local seed production systems that work for smallholder farmers, and broad-based information distribution (e.g. learning DVDs), it is possible to increase adoption rates and reach a much larger scale of smallholder farmers. Hence, plant breeding itself is merely a research methodology. Only if it is integrated in the respective cultural and socio-economic context it can contribute to the entire agricultural production system by providing improved seeds.

The future challenge of increasing food production with decreasing P-resources can only be tackled if all stakeholders in the supply and demand chain take action and devote more efforts to sustaining the remaining P resources, hence closing the nutrient cycle of our current food production system.

Summary

A growing world population juxtaposed with dwindling phosphorus (P) resources present new challenges to current and future global agricultural production. The burden of depleting phosphorus resources is particularly felt in sub-Saharan Africa (SSA). The expected doubling of its population by 2050 and the widespread poor soil fertility will pose an enormous task to future food security in SSA. Plant breeding can be considered as one major factor to improve agricultural production under these harsh low-input conditions. Nevertheless, until recently there have been no thorough breeding efforts to enhance crop production for low-P soil conditions in SSA.

Sorghum (*Sorghum bicolor* L. Moench) is the world's fifth and Africa's second most grown cereal crop. Sorghum is a staple crop of SSA and is mostly grown in resource poor regions under low-input cropping conditions, with the largest share in West Africa (WA). Its good adaptation to harsh environmental conditions makes it an important crop for the arid and semi-arid regions, hence a crop vital for food security and increasingly farm income in WA. Breeding sorghum specifically targeting P-limited soils is considered as one of the major challenges for future food production and can serve millions of smallholder farmers in WA. Nevertheless, plant breeders are mostly reluctant to conduct breeding experiments under low-input conditions due to a higher spatial variability of soil properties leading to a lower response to selection.

In an unprecedented large scale multi-environment experiment from 2006-2012 in three WA countries, namely Mali, Senegal and Niger, 187 WA sorghum genotypes were evaluated for their performance under P-sufficient and P-deficient conditions. The main goal of this study was to establish a breeding strategy for sorghum targeting P-limited environments. In order to establish such a strategy, the following objectives were defined: (I) to evaluate the impact of spatial models on genotypic selection in low-input field trials, (II) to develop a selection strategy for sorghum targeting P-limited environments, based on quantitative genetic parameters and (III) to identify genomic regions influencing sorghum performance in P-limited environments using modern genomic tools.

The major findings of this study can be summarized as follows:

Spatial models can increase the precision and efficiency especially of low-input field trials and may lead to different genotype rankings. Hence spatial models and/or adequate field designs are necessary tools for efficient genotype selection under low-input conditions and must be considered in a breeding program targeting P-limited conditions.

Sorghum performance is severely impeded by low-P soil conditions and shows large grain yield and plant height reductions and delayed flowering. Nevertheless, WA sorghum is generally well adapted to low-P soil conditions and shows a large exploitable genetic variation for P efficiency. Direct selection under low-P conditions is feasible, necessary and more efficient than indirect selection under high-P conditions and should be pursued in a breeding program targeting P-limited environments. Landrace genotypes are more specifically adapted to low-P conditions and show a higher P acquisition capacity, Durra and Guinea race sorghums show a similar specific low-P adaptation, hence these genotype groups are very promising source germplasm for further breeding efforts. Photoperiod sensitive genotypes show less delay in heading, a higher P acquisition rate and a specific low-P adaptation, hence should be considered for climate and low-P resilience breeding. Selection for low P concentration of grain can be used to enhance internal P use efficiency, therefore decreasing further soil P mining. WA sorghum shows a large genetic diversity, hence providing a valuable source for genetic studies examining the underlying genetics of low-P adaptation.

There are many genomic regions involved in sorghum adaptation to low-P soil conditions. Nevertheless, some regions could be identified as major contributors, showing large effects on and strong associations to genotypic performance. Molecular markers in sorghum homologs of the major P efficiency gene *PSTOL1* from rice stably enhanced P uptake and crop performance through an increased root growth of sorghum under low-P soil conditions and can be used in marker assisted selection for grain yield production under P-limited conditions. Furthermore, it was observed that grain yield production under P-limited conditions and Al-tolerance are pleiotropically regulated by the same genomic region and most probably the same gene *SbMATE*. Molecular markers of this region and within the gene *SbMATE* should be used for marker assisted selection to simultaneously enhance the tolerance to two of the most serious abiotic stresses for sorghum in WA, Al toxicity and P deficiency. WA Guinea race sorghums are an excellent source not only for low-P specific alleles, but also for Al-

tolerance and represent therefore an excellent source germplasm for allele mining and marker assisted selection. Genomic selection appears to be a very promising approach to further increase the response to selection. But methods giving more weight to single molecular markers linked to Al-tolerance should be considered.

The laid out results show that breeding sorghum specifically targeting P-limited conditions is necessary and feasible using advanced statistical models and modern genetic tools, and should be pursued as a major selection criterion in WA sorghum breeding programs. Nevertheless, only by combining agronomic and socio-economic measures with plant breeding efforts, millions of WA smallholder farmers can be reached and major yield increases can be expected in the near future.

Zusammenfassung

Die Weltbevölkerung wächst, die Phosphor (P) - Lagerstätten verringern sich: damit ist die derzeitige und vor allem zukünftige globale Landwirtschaft vor neue Herausforderungen gestellt. Das Problem der sich erschöpfenden P-Ressourcen wird speziell in Sub-Sahara Afrika (SSA) wahrgenommen. Die dort besonders stark zunehmende Bevölkerung und die weitverbreitete geringe Bodenfruchtbarkeit stellen eine enorme Aufgabe für die zukünftige Ernährungssicherheit in SSA dar. Hier kann die Pflanzenzüchtung potentiell einen großen Beitrag zur Steigerung der landwirtschaftlichen Produktion unter diesen rauen und extensiven Produktionsbedingungen leisten. Trotzdem wurden bis vor kurzem noch keine breiter angelegten Züchtungsvorhaben zur verbesserten Pflanzenproduktion unter P-Mangelbedingungen in SSA durchgeführt.

Im Getreideanbau steht Sorghum (*Sorghum bicolor* (L.) Moench) in Afrika an zweiter und weltweit an fünfter Stelle. Sorghum ist ein wichtiges Grundnahrungsmittel in SSA und wird vor allem in ressourcenschwachen Regionen, hauptsächlich in West Afrika (WA), unter extensiven Anbaubedingungen kultiviert. Die gute Anpassung an widrige Umweltbedingungen macht Sorghum zu einer lebenswichtigen Kulturpflanze für die ariden und semi-ariden Regionen, und somit leistet speziell dieses Getreide einen entscheidenden Beitrag zur Ernährungssicherung. Außerdem verbessert der Anbau von Sorghum auch zunehmend die Einkommenslage vieler Kleinbauern in WA. Daher könnte eine Sorghum-Züchtung, die speziell auf diese P-Mangelbedingungen ausgerichtet ist, der zukünftigen Nahrungsmittelsicherung und Millionen von Kleinbauern in WA dienen. Jedoch stehen viele Pflanzenzüchter Selektionsexperimenten unter extensiven Anbaubedingungen ablehnend gegenüber, da hier meist eine höhere Variation von Bodeneigenschaften vorherrscht und somit ein geringerer Zuchterfolg zu erwarten ist.

In einer beispiellosen, groß angelegten mehr-ortigen Versuchsserie von 2006-2012 in drei WA Ländern, namentlich Mali, Niger und Senegal, wurden 187 WA Sorghum Genotypen hinsichtlich ihrer Leistung auf Böden mit P-Mangel sowie auf Böden mit ausreichender P-Düngung untersucht. Hauptziel dieser Studie war die Entwicklung einer effizienten Züchtungsstrategie für eine verbesserte Anpassung von Sorghum an P-Mangelstandorte in WA. Um solch eine Strategie darzulegen wurden folgende Ziele genauer untersucht: (I) Einfluss geostatistischer Methoden

zum Ausgleich der Feldheterogenität auf die Güte genotypischer Selektion unter extensiven Anbaubedingungen, (II) Entwicklung einer auf quantitativ-genetischen Parameteren basierenden Selektionsstrategie für Sorghum-Züchtung unter P-Mangelbedingungen und (III) Identifikation von an der Anpassung von Sorghum an P-Mangelbedingungen beteiligten Genomregionen mittels modernster Genotypisierungsmethoden.

Die wichtigsten Erkenntnisse dieser Studie können folgendermaßen zusammengefasst werden:

Geostatistische Adjustierung kann speziell unter extensiven Anbaubedingungen die Präzision und Heritabilität der genotypischen Unterschiede erhöhen und zu einer unterschiedlichen Rangordnung der Genotypen führen. Daher sind geostatistische Analysen und/oder angepasste Versuchsdesigns notwendige Methoden für eine effiziente genotypische Selektion unter extensiven Anbaubedingungen und sollten auf jeden Fall in einem Zuchtprogramm für P-Mangelbedingungen beachtet werden.

Das Wachstum von Sorghum ist unter P-Mangelbedingungen sehr beeinträchtigt, dies zeigt sich in einem stark reduzierten Ertrag, einer verringerten Pflanzenhöhe und einem späteren Blühzeitpunkt. Dennoch zeigt Sorghum aus WA eine sehr gute allgemeine Anpassung an P-Mangelbedingungen und eine breite züchterisch nutzbare genetische Vielfalt für P-Effizienz. Eine direkte Selektion unter P-Mangelbedingungen ist notwendig, durchführbar und effizienter als eine indirekte Selektion unter gut mit P gedüngten Bedingungen und sollte daher in einem Zuchtprogram für P-Mangelbedingungen berücksichtigt werden. Genotypen, welche als Landrassen klassifiziert wurden, zeigten eine bessere Anpassung an P-Mangelbedingungen auf und haben die Fähigkeit mehr P aus dem Boden aufzunehmen. Durra und Guinea Sorghum Rassen weisen eine vergleichbare spezifische Anpassung für P-Mangelbedingungen auf und somit stellen diese Genotyp-Gruppen eine wichtige Quelle für weitere Zuchtarbeiten dar. Photoperiodisch sensible Genotypen hatten eine geringere Blühzeitverzögerung, eine bessere P Aneignungsfähigkeit und eine allgemein spezifischere Anpassung an P-Mangelbedingungen. Demzufolge sollten photoperiodisch sensible Genotypen speziell in einer Züchtung für eine verbesserte Klima- und P-Mangel Resilienz verwendet werden. Durch die Selektion auf eine verringerte P Konzentration im Korn kann die interne P Nutzungseffizienz gesteigert und somit eine weitere Reduktion der Bodenfruchtbarkeit verringert werden. WA Sorghum weist eine sehr breite genetische Vielfalt auf und stellt somit eine wertvolle Quelle für genetische Studien zur Anpassung an P-Mangelbedingungen dar.

Eine Vielzahl von genomischen Regionen ist an der Anpassung von Sorghum an P-Mangelbedingungen beteiligt. Trotzdem wurden einige genomische Regionen identifiziert, welche große Effekte auf und eine enge Assoziation zur genotypischen Leistung zeigten. Durch molekulare Marker in Sorghum Homologen des Haupt-P-Effizienz Genes *PSTOL1* aus Reis konnte die verbesserte P-Aufnahme aufgrund eines stärkeren Wurzelwachstums von Sorghum unter P-Mangelbedingungen erklärt werden. Somit können diese Marker zur markergestützten Selektion hinsichtlich Ertragssteigerung verwendet werden. Des weiteren wurde festgestellt, dass Kornertrag unter P-Mangelbedingungen und Aluminium-Toleranz von der gleichen genomischen Region pleiotropisch reguliert sind und höchstwahrscheinlich auch von demselben Gen *SbMATE*. Molekulare Marker dieser Region und innerhalb des Gens *SbMATE* sollten daher für eine markergestützte Selektion verwendet werden, um eine simultane Verbesserung der Toleranz gegenüber den zwei wichtigsten abiotischen Stressfaktoren, Al-Toxizität und P-Mangel, in WA Sorghum zu erreichen. WA Sorghum der Guinea Rasse erwies sich als eine Hauptquelle für P-Mangel- als auch für Al-Toleranz spezifischer Allele. Es bietet somit einen exzellenten genetischen Grundstock für das Auffinden von Allelen und zur markergestützen Selektion. Desweiteren erwies sich die genomweite Selektion als eine sehr vielversprechende Methode um den Zuchtfortschritt zu steigern, jedoch sollten Methoden, welche einzelnen molekularen Markern ein größeres Gewicht geben, in Betracht gezogen werden.

Die dargestellten Resultate zeigen, dass eine Sorghum-Züchtung speziell für P-Mangelbedingungen notwendig und mit Hilfe von fortgeschrittenen statistischen Modellen und modernen genetischen Methoden effizient durchführbar ist. Eine spezielle Züchtung für P-Mangelbedingungen sollte ein Hauptselektionsmerkmal in WA Sorghum-Züchtungs-programmen sein. Jedoch können große Ertragssteigerungen bei Millionen von Kleinbauern in der nahen Zukunft nur erreicht werden, wenn pflanzenzüchterische Anstrengungen zusammen mit agronomischen und sozio-ökonomischen Maßnahmen realisiert werden.

References

Araújo, A.P., and M.G. Teixeira. 2003. Nitrogen and phosphorus harvest indices of common bean cultivars: Implications for yield quantity and quality. Plant Soil. 257: 425–433. doi:10.1023/A:1027353822088.

Atlin, G.N., and K.J. Frey. 1989. Predicting the relative effectiveness of direct versus indirect selection for oat yield in three types of stress environments. Euphytica. 44: 137–142. doi:10.1007/BF00022608.

Beebe, S., J. Lynch, N. Galwey, J. Tohme, and I. Ochoa. 1997. A geographical approach to identify phosphorus-efficient genotypes among landraces and wild ancestors of common bean. Euphytica. 95: 325–338.

Billot, C., P. Ramu, S. Bouchet, J. Chantereau, M. Deu, L. Gardes, J.-L. Noyer, J.-F. Rami, R. Rivallan, Y. Li, P. Lu, T. Wang, R.T. Folkertsma, E. Arnaud, H.D. Upadhyaya, J.-C. Glaszmann, and C.T. Hash. 2013. Massive Sorghum Collection Genotyped with SSR Markers to Enhance Use of Global Genetic Resources. PLoS ONE. 8: e59714. doi:10.1371/journal.pone.0059714.

Birner, R., S.A. Kone, N. Linacre, and D. Resnick. 2007. Biofortified Foods and Crops in West Africa: Mali and Burkina Faso. AgBioForum Vol 10 No 3 2007.

Brachi, B., G.P. Morris, and J.O. Borevitz. 2011. Genome-wide association studies in plants: the missing heritability is in the field. Genome Biol. 12: 232. doi:10.1186/gb-2011-12-10-232.

Vom Brocke, K., G. Trouche, E. Weltzien, C.P. Barro-Kondombo, E. Gozé, and J. Chantereau. 2010. Participatory variety development for sorghum in Burkina Faso: Farmers' selection and farmers' criteria. Field Crops Res. 119: 183–194. doi:10.1016/j.fcr.2010.07.005.

Brouwer, J., L.K. Fussell, and L. Herrmann. 1993. Soil and crop growth micro-variability in the West African semi-arid tropics: a possible risk-reducing factor for subsistence farmers. Agric. Ecosyst. Environ. 45: 229–238.

Buerkert, A., A. Bationo, and H.-P. Piepho. 2001. Efficient phosphorus application strategies for increased crop production in sub-Saharan West Africa. Field Crops Res. 72: 1–15. doi:10.1016/S0378-4290(01)00166-6.

Burger, H., M. Schloen, W. Schmidt, and H.H. Geiger. 2008. Quantitative genetic studies on breeding maize for adaptation to organic farming. Euphytica. 163: 501–510. doi:10.1007/s10681-008-9723-4.

Caniato, F.F., C.T. Guimarães, M. Hamblin, C. Billot, J.F. Rami, B. Hufnagel, L.V. Kochian, J. Liu, A.A.F. Garcia, and C.T. Hash. 2011. The relationship between population structure and aluminum tolerance in cultivated sorghum. PloS One. 6: e20830.

Caniato, F.F., M.T. Hamblin, C.T. Guimaraes, Z. Zhang, R.E. Schaffert, L.V. Kochian, and J.V. Magalhaes. 2014. Association Mapping Provides Insights into the Origin and the Fine Structure of the Sorghum Aluminum Tolerance Locus, AltSB. PLoS ONE. 9: e87438. doi:10.1371/journal.pone.0087438.

Ceccarelli, S. 1989. Wide adaptation: how wide? Euphytica. 40: 197–205.

Ceccarelli, S. 1994. Specific adaptation and breeding for marginal conditions. Euphytica. 77: 205–219. doi:10.1007/BF02262633.

Ceccarelli, S. 1996. Adaptation to low/high input cultivation. Euphytica. 92: 203–214.

CGIAR, and W.A. Stoop. 2002. A Study and Comprehensive Analysis of the Causes for Low Adoption Rates of Agricultural Research Results in West and Central Africa : Possible Solutions Leading to Greater Future Impacts - the Mali and Guinea Case Studies. Available at: http://library.cgiar.org/handle/10947/84 (verified 24 February 2014)

Chen, J., L. Xu, Y. Cai, and J. Xu. 2008. QTL mapping of phosphorus efficiency and relative biologic characteristics in maize (Zea mays

L.) at two sites. Plant Soil. 313: 251–266. doi:10.1007/s11104-008-9698-x.

Chin, J.H., R. Gamuyao, C. Dalid, M. Bustamam, J. Prasetiyono, S. Moeljopawiro, M. Wissuwa, and S. Heuer. 2011. Developing Rice with High Yield under Phosphorus Deficiency: Pup1 Sequence to Application. Plant Physiol. 156: 1202 –1216. doi:10.1104/pp.111.175471.

Chin, J.H., X. Lu, S.M. Haefele, R. Gamuyao, A. Ismail, M. Wissuwa, and S. Heuer. 2009. Development and application of gene-based markers for the major rice QTL Phosphorus uptake 1. Theor. Appl. Genet. 120: 1073–1086. doi:10.1007/s00122-009-1235-7.

Cichy, K.A., S.S. Snapp, and M.W. Blair. 2008. Plant growth habit, root architecture traits and tolerance to low soil phosphorus in an Andean bean population. Euphytica. 165: 257–268. doi:10.1007/s10681-008-9778-2.

Cleland, J. 2013. World Population Growth; Past, Present and Future. Environ. Resour. Econ. 55: 543–554. doi:10.1007/s10640-013-9675-6.

Clerget, B., M. Dingkuhn, E. Goze, H.F.W. Rattunde, and B. Ney. 2008. Variability of phyllochron, plastochron and rate of increase in height in photoperiod-sensitive sorghum varieties. Ann. Bot. 101: 579–594. doi:10.1093/aob/mcm327.

Cooper, J., R. Lombardi, D. Boardman, and C. Carliell-Marquet. 2011. The future distribution and production of global phosphate rock reserves. Resour. Conserv. Recycl. 57: 78–86.

Cordell, D., J.-O. Drangert, and S. White. 2009. The story of phosphorus: Global food security and food for thought. Glob. Environ. Change. 19: 292–305. doi:10.1016/j.gloenvcha.2008.10.009.

Cordell, D., and S. White. 2013. Sustainable Phosphorus Measures: Strategies and Technologies for Achieving Phosphorus Security. Agronomy. 3: 86–116. doi:10.3390/agronomy3010086.

Delhaize, E., P. Taylor, P.J. Hocking, R.J. Simpson, P.R. Ryan, and A.E. Richardson. 2009. Transgenic barley (Hordeum vulgare L.) expressing the wheat aluminium resistance gene (TaALMT1) shows enhanced phosphorus nutrition and grain production when grown on an acid soil. Plant Biotechnol. J. 7: 391–400. doi:10.1111/j.1467-7652.2009.00403.x.

Deu, M., F. Sagnard, J. Chantereau, C. Calatayud, D. Hérault, C. Mariac, J.-L. Pham, Y. Vigouroux, I. Kapran, P.S. Traore, A. Mamadou, B. Gerard, J. Ndjeunga, and G. Bezançon. 2008. Niger-wide assessment of in situ sorghum genetic diversity with microsatellite markers. Theor. Appl. Genet. 116: 903–913. doi:10.1007/s00122-008-0721-7.

Ding, G., Z. Zhao, Y. Liao, Y. Hu, L. Shi, Y. Long, and F. Xu. 2012. Quantitative trait loci for seed yield and yield-related traits, and their responses to reduced phosphorus supply in Brassica napus. Ann. Bot. 109: 747–759. doi:10.1093/aob/mcr323.

Dingkuhn, M., B.B. Singh, B. Clerget, J. Chantereau, and B. Sultan. 2006. Past, present and future criteria to breed crops for water-limited environments in West Africa. Agric. Water Manag. 80: 241–261. doi:10.1016/j.agwat.2005.07.016.

Doumbia, M.D., L.R. Hossner, and A.B. Onken. 1993. Variable sorghum growth in acid soils of subhumid West Africa. Arid Soil Res. Rehabil. 7: 335–346. doi:10.1080/15324989309381366.

Edmondson, R.N. 2005. Past developments and future opportunities in the design and analysis of crop experiments. J. Agric. Sci. 143: 27–33. doi:10.1017/S0021859604004472.

Elshire, R.J., J.C. Glaubitz, Q. Sun, J.A. Poland, K. Kawamoto, E.S. Buckler, and S.E. Mitchell. 2011. A Robust, Simple Genotyping-by-Sequencing (GBS) Approach for High Diversity Species. PLoS ONE. 6: e19379. doi:10.1371/journal.pone.0019379.

Endelman, J.B. 2011. Ridge Regression and Other Kernels for Genomic Selection with R Package rrBLUP. Plant Genome J. 4: 250. doi:10.3835/plantgenome2011.08.0024.

Eswaran, H., E. van den Berg, and P. Reich. 1993. Organic carbon in soils of the world. Soil Sci Soc Am J. 57: 192–194.

Fageria, N.K., R.J. Wright, and V.C. Baligar. 1988. Rice cultivar evaluation for phosphorus use efficiency. Plant Soil. 111: 105–109. doi:10.1007/BF02182043.

Famoso, A.N., K. Zhao, R.T. Clark, C.-W. Tung, M.H. Wright, C. Bustamante, L.V. Kochian, and S.R. McCouch. 2011. Genetic Architecture of Aluminum Tolerance in Rice (Oryza sativa) Determined through Genome-Wide Association Analysis and QTL Mapping. PLoS Genet. 7: e1002221. doi:10.1371/journal.pgen.1002221.

Fang, Z., C. Shao, Y. Meng, P. Wu, and M. Chen. 2009. Phosphate signaling in Arabidopsis and Oryza sativa. Plant Sci. 176: 170–180. doi:10.1016/j.plantsci.2008.09.007.

FAO. 2012. FAO-Statistics. Available at: http://faostat.fao.org/site/567/DesktopDefault.aspx?PageID=567#ancor

FAO/IIASA/ISRIC/ISS-CAS/JRC. 2012. Harmonized World Soil Database (version 1.2). FAO, Rome, Italy and IIASA, Laxenburg, Austria. FAO, Rome, Italy and IIASA, Laxenburg, Austria.

Gallais, A., M. Coque, and P. Bertin. 2008. Response to selection of a maize population for adaptation to high or low nitrogen fertilization. Maydica. 53: 21–28.

Gamuyao, R., J.H. Chin, J. Pariasca-Tanaka, P. Pesaresi, S. Catausan, C. Dalid, I. Slamet-Loedin, E.M. Tecson-Mendoza, M. Wissuwa, and S. Heuer. 2012. The protein kinase Pstol1 from traditional rice confers tolerance of phosphorus deficiency. Nature. 488: 535–539. doi:10.1038/nature11346.

Gilmour, A.R., B.R. Cullis, and A.P. Verbyla. 1997. Accounting for Natural and Extraneous Variation in the Analysis of Field Experiments. J. Agric. Biol. Environ. Stat. 2: 269–293.

Grondona, M.O., J. Crossa, P.N. Fox, and W.H. Pfeiffer. 1996. Analysis of Variety Yield Trials Using Two-Dimensional Separable ARIMA Processes. Biometrics. 52: 763–770.

Hammond, J.P., M.R. Broadley, P.J. White, G.J. King, H.C. Bowen, R. Hayden, M.C. Meacham, A. Mead, T. Overs, W.P. Spracklen, and D.J. Greenwood. 2009. Shoot yield drives phosphorus use efficiency in Brassica oleracea and correlates with root architecture traits. J. Exp. Bot. 60: 1953 –1968. doi:10.1093/jxb/erp083.

Hammond, J.P., and P.J. White. 2011. Sugar Signaling in Root Responses to Low Phosphorus Availability. Plant Physiol. 156: 1033–1040. doi:10.1104/pp.111.175380.

Harlan, J.R., and J.M.J. de Wet. 1972. A Simplified Classification of Cultivated Sorghum. Crop Sci. 12: 172–176. doi:10.2135/cropsci 1972.0011183X001200020005x.

Haussmann, B.I.G., H. Fred Rattunde, E. Weltzien-Rattunde, P.S.C. Traoré, K. vom Brocke, and H.K. Parzies. 2012. Breeding strategies for adaptation of pearl millet and sorghum to climate variability and change in West Africa. J. Agron. Crop Sci. 198: 327–339. doi:10.1111/j.1439-037X.2012.00526.x.

Haynes, R.J., and M.S. Mokolobate. 2001. Amelioration of Al toxicity and P deficiency in acid soils by additions of organic residues: a critical review of the phenomenon and the mechanisms involved. Nutr. Cycl. Agroecosystems. 59: 47–63. doi:10.1023/A:1009823600950.

Heffner, E.L., A.J. Lorenz, J.-L. Jannink, and M.E. Sorrells. 2010. Plant Breeding with Genomic Selection: Gain per Unit Time and Cost. Crop Sci. 50: 1681. doi:10.2135/cropsci2009.11.0662.

Henry, A., P.J.A. Kleinman, and J.P. Lynch. 2008. Phosphorus runoff from a phosphorus deficient soil under common bean (Phaseolus vulgaris L.) and soybean (Glycine max L.) genotypes with contrasting root architecture. Plant Soil. 317: 1–16. doi:10.1007/ s11104-008-9784-0.

Henzell, R.G., and D.R. Jordan. 2009. Grain Sorghum Breeding. p. 183–197. *In* Carena, M.J. (ed.), Cereals. 1st ed. Springer.

Hirschhorn, J.N., K. Lohmueller, E. Byrne, and K. Hirschhorn. 2002. A comprehensive review of genetic association studies. Genet. Med. 4: 45–61. doi:10.1097/00125817-200203000-00002.

Holford, I.C.R. 1997. Soil phosphorus: its measurement, and its uptake by plants. Aust J Soil Res. 35: 227–240.

Horst, W.J., M. Kamh, J.M. Jibrin, and V.O. Chude. 2001. Agronomic measures for increasing P availability to crops. Plant Soil. 237: 211–223. doi:10.1023/A:1013353610570.

Hufnagel, B., S.M. Sousa, L. Assis, C.T. Guimaraes, W.L. Leiser, G. Corradi, B. Negri, B.G. Larson, J.E. Shaff, M.M. Pastina, E. Weltzien, H.F.W. Rattunde, J.H. Viana, R. Clark, A. Falcao, R. Gazaffi, A.A.F. Garcia, R.E. Schaffert, L.V. Kochian, and J.V. Magalhaes. 2014. Duplicate and conquer: multiple homologs of phosphorus starvation tolerance 1 enhance phosphorus acquisition and sorghum performance on low-P soils. Plant Physiol. *In Review.*

Hurrell, R.F., M.B. Reddy, M.-A. Juillerat, and J.D. Cook. 2003. Degradation of phytic acid in cereal porridges improves iron absorption by human subjects. Am. J. Clin. Nutr. 77: 1213–1219.

Ila'ava, V.P., P. Blamey, and C.J. Asher. 2000. Effects of lime and gypsum on growth of sweet potato in two strongly acid soils. Aust. J. Agric. Res. 51: 1031–1038.

Jannink, J.-L., A.J. Lorenz, and H. Iwata. 2010. Genomic selection in plant breeding: from theory to practice. Brief. Funct. Genomics. 9: 166–177. doi:10.1093/bfgp/elq001.

Jasinski, S.M. 2013. Phosphat Rock. Available at: http://minerals.usgs.gov/minerals/pubs/commodity/phosphate_rock/mcs-2012-phosp.pdf (verified 3 January 2014)

Jones, G.P.D., G.J. Blair, and R.S. Jessop. 1989. Phosphorus efficiency in wheat — A useful selection criterion? Field Crops Res. 21: 257–264. doi:10.1016/0378-4290(89)90007-5.

Kochian, L.V. 2012. Plant nutrition: Rooting for more phosphorus. Nature. 488: 466–467. doi:10.1038/488466a.

Kochian, L.V., O.A. Hoekenga, and M.A. Pineros. 2004. How do crop plants tolerate acid soils? Mechanism of aluminum tolerance and phosphorus efficiency. Annu. Rev. Plant Biol. 55: 459–493. doi:10.1146/annurev.arplant.55.031903.141655.

Lado, B., I. Matus, A. Rodríguez, L. Inostroza, J. Poland, F. Belzile, A. del Pozo, M. Quincke, M. Castro, and J. von Zitzewitz. 2013. Increased Genomic Prediction Accuracy in Wheat Breeding Through Spatial Adjustment of Field Trial Data. G3 GenesGenomesGenetics. 3: 2105–2114. doi:10.1534/g3.113.0078 07.

Lafitte, H., G. Yongsheng, S. Yan, and Z.-K. Li. 2007. Whole plant responses, key processes, and adaptation to drought stress: the case of rice. J Exp Bot. 58: 169–175. doi:10.1093/jxb/erl101.

Leiser, W.L., H.F. Rattunde, H.-P. Piepho, and H.K. Parzies. 2012a. Getting the most out of sorghum low-input field trials in West Africa using spatial adjustment. J. Agron. Crop Sci. 198: 349–359. doi:10.1111/ j.1439-037X.2012.00529.x.

Leiser, W.L., H.F.W. Rattunde, H.-P. Piepho, E. Weltzien, A. Diallo, A.E. Melchinger, H.K. Parzies, and B.I.G. Haussmann. 2012b. Selection strategy for sorghum targeting phosphorus-limited environments in West Africa: analysis of multi-environment experiments. Crop Sci. 52: 2517–2527. doi:10.2135/cropsci2012.02.0139.

Leiser, W.L., H.F.W. Rattunde, E. Weltzien, N. Cisse, M. Abdou, A. Diallo, A.O. Touré, J.V. Magalhaes, and B.I.G. Haussmann. 2014a. Two in one sweep: Aluminum tolerance and grain yield in P-limited soils are associated to the same genomic region in West African Sorghum. BMC Plant Biol. 14: 206. doi:10.1186/s12870-014-0206-6

Leiser, W.L., H.F.W. Rattunde, E. Weltzien, and B.I.G. Haussmann. 2014b. Phosphorus uptake and use efficiency of diverse West and Central African sorghum genotypes under field conditions in Mali. Plant Soil. 377: 383–394. doi:10.1007/s11104-013-1978-4.

Li, L., C. Liu, and X. Lian. 2010. Gene expression profiles in rice roots under low phosphorus stress. Plant Mol. Biol. 72: 423–432. doi:10.1007/s11103-009-9580-0.

Li, J., Y. Xie, A. Dai, L. Liu, and Z. Li. 2009. Root and shoot traits responses to phosphorus deficiency and QTL analysis at seedling stage using introgression lines of rice. J. Genet. Genomics Yi Chuan Xue Bao. 36: 173–183. doi:10.1016/S1673-8527(08)60104-6.

Liang, C., M.A. Piñeros, J. Tian, Z. Yao, L. Sun, J. Liu, J. Shaff, A. Coluccio, L.V. Kochian, and H. Liao. 2013. Low pH, Aluminum, and Phosphorus Coordinately Regulate Malate Exudation through GmALMT1 to Improve Soybean Adaptation to Acid Soils. Plant Physiol. 161: 1347–1361. doi:10.1104/pp.112.208934.

Lynch, J.P. 2007. Roots of the Second Green Revolution. Aust. J. Bot. 55: 493–512. doi:10.1071/BT06118.

Lynch, J.P. 2011. Root Phenes for Enhanced Soil Exploration and Phosphorus Acquisition: Tools for Future Crops. Plant Physiol. 156: 1041 –1049. doi:10.1104/pp.111.175414.

Lynch, J.P., and K.M. Brown. 2008. Root strategies for phosphorus acquisition. p. 83–116. *In* The Ecophysiology of Plant-Phosphorus Interactions. Springer Netherlands.

Ma, J.F., P.R. Ryan, and E. Delhaize. 2001. Aluminium tolerance in plants and the complexing role of organic acids. Trends Plant Sci. 6: 273–278. doi:10.1016/S1360-1385(01)01961-6.

MacDonald, G.K., E.M. Bennett, P.A. Potter, and N. Ramankutty. 2011. Agronomic phosphorus imbalances across the world's croplands. Proc. Natl. Acad. Sci. 108: 3086–3091. doi:10.1073/pnas.1010808 108.

Magalhaes, J.V., J. Liu, C.T. Guimarães, U.G.P. Lana, V.M.C. Alves, Y.-H. Wang, R.E. Schaffert, O.A. Hoekenga, M.A. Piñeros, J.E. Shaff, P.E. Klein, N.P. Carneiro, C.M. Coelho, H.N. Trick, and L.V. Kochian. 2007. A gene in the multidrug and toxic compound extrusion (MATE) family confers aluminum tolerance in sorghum. Nat. Genet. 39: 1156–1161. doi:10.1038/ng2074.

Mandal, N.P., P.K. Sinha, M. Variar, V.D. Shukla, P. Perraju, A. Mehta, A.R. Pathak, J.L. Dwivedi, S.P.S. Rathi, S. Bhandarkar, B.N. Singh, D.N. Singh, S. Panda, N.C. Mishra, Y.V. Singh, R. Pandya, M.K. Singh, R.B.S. Sanger, J.C. Bhatt, R.K. Sharma, A. Raman, A. Kumar, and G. Atlin. 2010. Implications of genotype × input interactions in breeding superior genotypes for favorable and unfavorable rainfed upland environments. Field Crops Res. 118: 135–144. doi:10.1016/j.fcr.2010.05.004.

Manske, G.G.B., J.I. Ortiz-Monasterio, M. van Ginkel, R.M. González, R.A. Fischer, S. Rajaram, and P.L.G. Vlek. 2001. Importance of P uptake efficiency versus P utilization for wheat yield in acid and calcareous soils in Mexico. Eur. J. Agron. 14: 261–274. doi:10.1016/S1161-0301(00)00099-X.

Manu, A., L.P. Wilding, L.R. Hossner, A.A. Pfordresher, and S.C. Geiger. 1996. Soil Parameters Related to Crop Growth Variability in Western Niger, West Africa. Soil Sci. Soc. Am. J. 60: 283–288. doi:10.2136/sssaj1996.03615995006000010043x.

Marschner, H. 1995. Mineral nutrition of higher plants. Academic Press, London.

Massman, J.M., H.-J.G. Jung, and R. Bernardo. 2012. Genomewide Selection versus Marker-assisted Recurrent Selection to Improve Grain Yield and Stover-quality Traits for Cellulosic Ethanol in Maize. Crop Sci. 0: 0. doi:10.2135/cropsci2012.02.0112.

Mengel, K., and E.A. Kirkby. 2001. Principles of Plant Nutrition. 5th ed. Springer.

Meuwissen, T.H.E., B.J. Hayes, and M.E. Goddard. 2001. Prediction of Total Genetic Value Using Genome-Wide Dense Marker Maps. Genetics. 157: 1819–1829.

Moody, P.W., R.L. Aitken, and T. Dickson. 1998. Field amelioration of acidic soils in south-east Queensland. III. Relationships of maize yield response to lime and unamended soil properties. Aust. J. Agric. Res. 49: 649–656.

Morris, G.P., P. Ramu, S.P. Deshpande, C.T. Hash, T. Shah, H.D. Upadhyaya, O. Riera-Lizarazu, P.J. Brown, C.B. Acharya, S.E. Mitchell, J. Harriman, J.C. Glaubitz, E.S. Buckler, and S. Kresovich. 2013. Population genomic and genome-wide association studies of agroclimatic traits in sorghum. Proc. Natl. Acad. Sci. 110: 453–458. doi:10.1073/pnas.1215985110.

Mueller, N.D., J.S. Gerber, M. Johnston, D.K. Ray, N. Ramankutty, and J.A. Foley. 2012. Closing yield gaps through nutrient and water management. Nature. 490: 254–257. doi:10.1038/nature11420.

Mühleisen, J., J.C. Reif, H.P. Maurer, J. Möhring, and H.-P. Piepho. 2013. Visual Scorings of Drought Stress Intensity as Covariates for Improved Variety Trial Analysis. J. Agron. Crop Sci. 199: 321–330. doi:10.1111/jac.12025.

Neumann, G., and V. Römheld. 1999. Root excretion of carboxylic acids and protons in phosphorus-deficient plants. Plant Soil. 211: 121–130. doi:10.1023/A:1004380832118.

Nilsson, L., R. Müller, and T.H. Nielsen. 2010. Dissecting the plant transcriptome and the regulatory responses to phosphate deprivation. Physiol. Plant. 139: 129–143. doi:10.1111/j.1399-3054.2010.01356.x.

Nord, E.A., and J.P. Lynch. 2008. Delayed reproduction in Arabidopsis thaliana improves fitness in soil with suboptimal phosphorus availability. Plant Cell Environ. 31: 1432–1441. doi:10.1111/j.1365-3040.2008.01857.x.

Obersteiner, M., J. Peñuelas, P. Ciais, M. van der Velde, and I.A. Janssens. 2013. The phosphorus trilemma. Nat. Geosci. 6: 897–898.

Olatoye, M.O. 2013. Genetic assessment and identification of molecular markers for component traits contributing to Sorghum adaptation to low phosphorus conditions in West Africa. MSc-Thesis, University of Hohenheim, Germany.

Ozturk, L., S. Eker, B. Torun, and I. Cakmak. 2005. Variation in phosphorus efficiency among 73 bread and durum wheat genotypes grown in a phosphorus-deficient calcareous soil. Plant Soil. 269: 69–80. doi:10.1007/s11104-004-0469-z.

Panigrahy, M., D.N. Rao, and N. Sarla. 2009. Molecular mechanisms in response to phosphate starvation in rice. Biotechnol. Adv. 27: 389–397. doi:10.1016/j.biotechadv.2009.02.006.

Parentoni, S., C. de Souza Jr, V. de Carvalho Alves, E. Gama, A. Coelho, A. de Oliveira, P. Guimarães, C. Guimarães, M. Vasconcelos, C.A.P. Pacheco, W.F. Meirelles, J.V. de Magalhães, L.J. Moreira Guimarães, A.R. da Silva, F. Ferreira Mendes, and R.E. Schaffert. 2010. Inheritance and breeding strategies for phosphorus efficiency in tropical maize (Zea Mays L.). Maydica. 55: 1–15.

Parentoni, S.N., and C.L. Souza Jr. 2008. Phosphorus acquisition and internal utilization efficiency in tropical maize genotypes. Pesqui. Agropecuária Bras. 43: 893–901.

Park, G.-G., J.-J. Park, J. Yoon, S.-N. Yu, and G. An. 2010. A RING finger E3 ligase gene, Oryza sativa Delayed Seed Germination 1 (OsDSG1), controls seed germination and stress responses in rice. Plant Mol. Biol. 74: 467–478. doi:10.1007/s11103-010-9687-3.

Paterson, A.H., J.E. Bowers, R. Bruggmann, I. Dubchak, J. Grimwood, H. Gundlach, G. Haberer, U. Hellsten, T. Mitros, A. Poliakov, J. Schmutz, M. Spannagl, H. Tang, X. Wang, T. Wicker, A.K. Bharti, J. Chapman, F.A. Feltus, U. Gowik, I.V. Grigoriev, E. Lyons, C.A. Maher, M. Martis, A. Narechania, R.P. Otillar, B.W. Penning, A.A. Salamov, Y. Wang, L. Zhang, N.C. Carpita, M. Freeling, A.R. Gingle, C.T. Hash, B. Keller, P. Klein, S. Kresovich, M.C. McCann,

R. Ming, D.G. Peterson, Mehboob-ur-Rahman, D. Ware, P. Westhoff, K.F.X. Mayer, J. Messing, and D.S. Rokhsar. 2009. The Sorghum bicolor genome and the diversification of grasses. Nature. 457: 551–556. doi:10.1038/nature07723.

Pavan, M.A., F.T. Bingham, and P.F. Pratt. 1984. Redistribution of exchangeable calcium, magnesium, and aluminum following lime or gypsum applications to a Brazilian Oxisol. Soil Sci. Soc. Am. J. 48: 33–38.

Ramu, P., B. Kassahun, S. Senthilvel, C. Ashok Kumar, B. Jayashree, R.T. Folkertsma, L.A. Reddy, M.S. Kuruvinashetti, B.I.G. Haussmann, and C.T. Hash. 2009. Exploiting rice–sorghum synteny for targeted development of EST-SSRs to enrich the sorghum genetic linkage map. Theor. Appl. Genet. 119: 1193–1204. doi:10.1007/s00122-009-1120-4.

Rattunde, H.F.W., E. Weltzien, B. Diallo, A.G. Diallo, M. Sidibe, A.O. Touré, A. Rathore, R.R. Das, W.L. Leiser, and A. Touré. 2013. Yield of photoperiod-sensitive sorghum hybrids based on Guinea-race germplasm under farmers' field conditions in Mali. Crop Sci. 53: 2454. doi:10.2135/cropsci2013.03.0182.

Richardson, A.E., J.P. Lynch, P.R. Ryan, E. Delhaize, F.A. Smith, S.E. Smith, P.R. Harvey, M.H. Ryan, E.J. Veneklaas, H. Lambers, A. Oberson, R.A. Culvenor, and R.J. Simpson. 2011. Plant and microbial strategies to improve the phosphorus efficiency of agriculture. Plant Soil. 349: 121–156. doi:10.1007/s11104-011-0950-4.

Riedelsheimer, C., J. Lisec, A. Czedik-Eysenberg, R. Sulpice, A. Flis, C. Grieder, T. Altmann, M. Stitt, L. Willmitzer, and A.E. Melchinger. 2012a. Genome-wide association mapping of leaf metabolic profiles for dissecting complex traits in maize. Proc. Natl. Acad. Sci. 109: 8872–8877. doi:10.1073/pnas.1120813109.

Riedelsheimer, C., F. Technow, and A.E. Melchinger. 2012b. Comparison of whole-genome prediction models for traits with contrasting genetic architecture in a diversity panel of maize inbred lines. BMC Genomics. 13: 452. doi:10.1186/1471-2164-13-452.

Rose, T.J., M.T. Rose, J. Pariasca-Tanaka, S. Heuer, and M. Wissuwa. 2011. The frustration with utilization: Why have improvements in internal phosphorus utilization efficiency in crops remained so elusive? Front. Plant Sci. 2 doi:10.3389/fpls.2011.00073.

Rose, T.J., and M. Wissuwa. 2012. Rethinking internal phosphorus utilization efficiency. p. 185–217. *In* Advances in Agronomy. Elsevier.

Rossiter, R.C. 1978. Phosphorus deficiency and flowering in subterranean clover (T. subterraneum L.). Ann. Bot. 42: 325 –329.

Rouached, H., A.B. Arpat, and Y. Poirier. 2010a. Regulation of Phosphate Starvation Responses in Plants: Signaling Players and Cross-Talks. Mol. Plant. 3: 288–299. doi:10.1093/mp/ssp120.

Rouached, H., A.B. Arpat, and Y. Poirier. 2010b. Regulation of Phosphate Starvation Responses in Plants: Signaling Players and Cross-Talks. Mol. Plant. 3: 288 –299. doi:10.1093/mp/ssp120.

Sagnard, F., M. Deu, D. Dembélé, R. Leblois, L. Touré, M. Diakité, C. Calatayud, M. Vaksmann, S. Bouchet, Y. Mallé, S. Togola, and P.C.S. Traoré. 2011. Genetic diversity, structure, gene flow and evolutionary relationships within the Sorghum bicolor wild–weedy–crop complex in a western African region. Theor. Appl. Genet. 123: 1231–1246. doi:10.1007/s00122-011-1662-0.

Sattari, S.Z., A.F. Bouwman, K.E. Giller, and M.K. van Ittersum. 2012. Residual soil phosphorus as the missing piece in the global phosphorus crisis puzzle. Proc. Natl. Acad. Sci. 109: 6348–6353. doi:10.1073/pnas.1113675109.

Secco, D., A. Baumann, and Y. Poirier. 2010. Characterization of the Rice PHO1 Gene Family Reveals a Key Role for OsPHO1;2 in Phosphate Homeostasis and the Evolution of a Distinct Clade in Dicotyledons. Plant Physiol. 152: 1693–1704. doi:10.1104/pp.109. 149872.

Shimizu, A., K. Kato, A. Komatsu, K. Motomura, and H. Ikehashi. 2008. Genetic analysis of root elongation induced by phosphorus deficiency in rice (Oryza sativa L.): fine QTL mapping and multivariate analysis of related traits. Theor. Appl. Genet. 117: 987–996. doi:10.1007/s00122-008-0838-8.

Simmonds, N. 1991. Selection for local adaptation in a plant breeding programme. Theor. Appl. Genet. 82: 363–367. doi:10.1007/BF 02190624.

Simpson, R.J., A. Oberson, R.A. Culvenor, M.H. Ryan, E.J. Veneklaas, H. Lambers, J.P. Lynch, P.R. Ryan, E. Delhaize, F.A. Smith, S.E. Smith, P.R. Harvey, and A.E. Richardson. 2011. Strategies and agronomic interventions to improve the phosphorus-use efficiency of farming systems. Plant Soil. 349: 89–120. doi:10.1007/s11104-011-0880-1.

Singh, M., R.S. Malhotra, S. Ceccarelli, A. Sarker, S. Grando, and W. Erskine. 2003. Spatial variability models to improve dryland field trials. Exp. Agric. 39: 151–160. doi:10.1017/S0014479702001175.

Soderlund, C., W. Nelson, A. Shoemaker, and A. Paterson. 2006. SyMAP: A system for discovering and viewing syntenic regions of FPC maps. Genome Res. 16: 1159–1168. doi:10.1101/gr.5396706.

Stoorvogel, J.J., E.M.A. Smaling, and B.H. Janssen. 1993. Calculating soil nutrient balances in Africa at different scales. Fertil. Res. 35: 227–235. doi:10.1007/BF00750641.

Topp, C.N., A.S. Iyer-Pascuzzi, J.T. Anderson, C.-R. Lee, P.R. Zurek, O. Symonova, Y. Zheng, A. Bucksch, Y. Mileyko, T. Galkovskyi, B.T. Moore, J. Harer, H. Edelsbrunner, T. Mitchell-Olds, J.S. Weitz, and P.N. Benfey. 2013. 3D phenotyping and quantitative trait locus mapping identify core regions of the rice genome controlling root architecture. Proc. Natl. Acad. Sci. 110: E1695–E1704. doi:10. 1073/pnas.1304354110.

Torabi, S., M. Wissuwa, M. Heidari, M.-R. Naghavi, K. Gilany, M.-R. Hajirezaei, M. Omidi, B. Yazdi-Samadi, A.M. Ismail, and G.H. Salekdeh. 2009. A comparative proteome approach to decipher the mechanism of rice adaptation to phosphorous deficiency. PROTEOMICS. 9: 159–170. doi:10.1002/pmic.200800350.

Turk, M.A., A.M. Tawaha, and M.K.J. El Shatnawi. 2003. Response of lentil (Lens culinaris Medik) to plant density, sowing date, phosphorus fertilization and ethephon application in the absence of moisture stress. J. Agron. Crop Sci. 189: 1–6. doi:10.1046/j.1439-037X.2003.00002.x.

Vaccari, D.A. 2009. Phosphorus: A Looming Crisis. Sci. Am. 300: 54–59.

Vance, C.P., C. Uhde-Stone, and D.L. Allan. 2003. Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. New Phytol. 157: 423–447.

Van der Velde, M., C. Folberth, J. Balkoviç, P. Ciais, S. Fritz, I.A. Janssens, M. Obersteiner, L. See, R. Skalský, W. Xiong, and J. Peñuelas. 2014. African crop yield reductions due to increasingly unbalanced Nitrogen and Phosphorus consumption. Glob. Change Biol. n/a–n/a. doi:10.1111/gcb.12481.

Van der Velde, M., L. See, L. You, J. Balkovič, S. Fritz, N. Khabarov, M. Obersteiner, and S. Wood. 2013. Affordable Nutrient Solutions for Improved Food Security as Evidenced by Crop Trials. PLoS ONE. 8: e60075. doi:10.1371/journal.pone.0060075.

Veneklaas, E.J., H. Lambers, J. Bragg, P.M. Finnegan, C.E. Lovelock, W.C. Plaxton, C.A. Price, W.-R. Scheible, M.W. Shane, P.J. White, and J.A. Raven. 2012. Opportunities for improving phosphorus-use efficiency in crop plants. New Phytol. 195: 306–320. doi:10.1111/j.1469-8137.2012.04190.x.

Voortman, R.L., and J. Brouwer. 2003. An empirical analysis of the simultaneous effects of nitrogen, phosphorus and potassium in millet production on spatially variable fields in SW Niger. Nutr. Cycl. Agroecosystems. 66: 143–164.

Voortman, R.L., J. Brouwer, and P.J. Albersen. 2004. Characterization of spatial soil variability and its effect on millet yield on Sudano-Sahelian coversands in SW Niger. Geoderma. 121: 65–82.

Wang, X., J. Shen, and H. Liao. 2010. Acquisition or utilization, which is more critical for enhancing phosphorus efficiency in modern crops? Plant Sci. 179: 302–306. doi:10.1016/j.plantsci.2010.06.007.

Wang, Y., H. Xu, J. Kou, L. Shi, C. Zhang, and F. Xu. 2013. Dual effects of transgenic Brassica napus overexpressing CS gene on tolerances to aluminum toxicity and phosphorus deficiency. Plant Soil. 362: 231–246. doi:10.1007/s11104-012-1289-1.

Weber, V.S., A.E. Melchinger, C. Magorokosho, D. Makumbi, M. Bänziger, and G.N. Atlin. 2012. Efficiency of Managed-Stress Screening of Elite Maize Hybrids under Drought and Low Nitrogen for Yield under Rainfed Conditions in Southern Africa. Crop Sci. 52: 1011–1020. doi:10.2135/cropsci2011.09.0486.

Wet, J.M.J.D., and J.R. Harlan. 1971. The origin and domestication of Sorghum bicolor. Econ. Bot. 25: 128–135. doi:10.1007/BF02860074.

Wimmer, V., C. Lehermeier, T. Albrecht, H.-J. Auinger, Y. Wang, and C.-C. Schön. 2013. Genome-Wide Prediction of Traits with Different Genetic Architecture Through Efficient Variable Selection. Genetics. 195: 573–587. doi:10.1534/genetics.113.150078.

Wissuwa, M., and N. Ae. 2001. Genotypic variation for tolerance to phosphorus deficiency in rice and the potential for its exploitation in rice improvement. Plant Breed. 120: 43–48. doi:10.1111/j.1439-0523.2001.tb01698.x.

Wissuwa, M., M. Yano, and N. Ae. 1998. Mapping of QTLs for phosphorus-deficiency tolerance in rice (Oryza sativa L.). Theor. Appl. Genet. 97: 777–783. doi:10.1007/s001220050955.

Zhang, F.S., J. Ma, and Y.P. Cao. 1997. Phosphorus deficiency enhances root exudation of low-molecular weight organic acids and utilization of sparingly soluble inorganic phosphates by radish (Raghanus satiuvs L.) and rape (Brassica napus L.) plants. Plant Soil. 196: 261–264. doi:10.1023/A:1004214410785.

Zhu, C., M. Gore, E.S. Buckler, and J. Yu. 2008. Status and Prospects of Association Mapping in Plants. Plant Genome J. 1: 5. doi:10.3835/plantgenome2008.02.0089.

Zongo, J.-D., P.H. Gouyon, and M. Sandmeier. 1993. Genetic variability among sorghum accessions from the Sahelian agroecological region of Burkina Faso. Biodivers. Conserv. 2: 627–636. doi:10.1007/BF00051963.

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