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With 1 figure and 2 tables

Abstract

Semi-arid and sub-humid West Africa is characterized by high inter-annual rainfall variability, with variable onset of the rainy season, somewhat more predictable endings, and drought or excess water occurrence at any time during the growing season. Climate change is predicted to increase this variability. This article summarizes options for plant breeders to enhance adaptation of pearl millet (*Pennisetum glaucum* [L.] R. Br.) and sorghum (*Sorghum bicolor* [L.] Moench) to climate variability in West Africa. Developing variety types with high degrees of heterozygosity and genetic heterogeneity for adaptation traits helps achieving better individual and population buffering capacity. Traits that potentially enhance adaptive phenotypic plasticity or yield stability in variable climates include photoperiod-sensitive flowering, plastic tillering, flooding tolerance, seedling heat tolerance, and phosphorus efficiency. Farmer-participatory dynamic genepool management using broad-based populations and diverse selection environments is useful to develop new diverse germplasm adapted to specific production constraints including climate variability. For sustainable productivity increase, improved cultivars should respond to farmer-adoptable soil fertility management and water harvesting techniques. Larger-scale, on-farm participatory testing will enable assessments of varietal performance under evolving climatic variability, provide perspective on needs and opportunities, and enhance adoption. Strengthening seed systems will be required to achieve sustainable impacts.

Keywords. Climate change and/or variability, heterozygosity, heterogeneity, phenotypic plasticity, buffering, dynamic genepool management

Running title: Adaptation to climate variability and change

Introduction

Pearl millet (*Pennisetum glaucum* [L.] R. Br.) and sorghum (*Sorghum bicolor* [L.] Moench) are major crops cultivated under rainfed conditions in the dryland areas of West Africa. Projections suggest that among main world crops, African millet and sorghum production will witness, by far, the fastest growth rate for the 2000-2050 period (Nelson et al. 2009). These cereals are most important for food security, especially in the West African Sudano-Sahelian belt, where they are grown as staple crops by some of the poorest people of the world. Smallholder subsistence farmers in African rainfed farming systems are considered to be highly vulnerable to climate change impacts (Jarvis et al. 2011). A review of projected effects on pearl millet and sorghum yields indicates 10-15% losses that become statistically significant during the second half of this century (Knox et al. 2011). Predicted increases in climate variability associated with expected climate change in West Africa require cereal breeders to develop crop improvement strategies that favor adaptation to this variability. The present article discusses options to achieve this challenge. It first considers the relevance of climate change and variability in semi-arid and sub-humid West Africa and consequences for setting breeding priorities. It then reviews mechanisms of adaptation to climate variability from a population-genetic point of view. The following aspects are then addressed that are pertinent to applied breeding activities:

- the role of the genetic structure of a cultivar;

- selection methods and traits for adaptation to climate variability;

- long-term development of adapted diversity using a dynamic genepool management approach;

- enhancing population buffering *via* system diversification;

- developing cultivars with specific adaptation to natural resource management techniques;

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- costs of adaptation to climate variability; and

- strengthening the adaptive capacities of farmers.

Relevance of climate change and variability for breeding in semi-arid and sub-humid West Africa

Three major climate variability modes control plant adaptation in semi-arid and sub-humid West Africa: the seasonal rainfall cycle and its inter-annual variability (high frequency), natural multi-decadal wetting and desiccation cycles (medium frequency), and long-term changes in moisture regimes associated with changes in temperature (low frequency). Natural climate change pertains to medium and low frequency modes. Anthropogenic climate change expresses mostly in the low frequency mode. Operating on different time scales, all three variability modes interact with each other in complex ways, many of which are not yet elucidated.

One important consequence constraining tropical dryland crop improvement for future climates is that confidence levels are highest for variables that only weakly control crop performance, particularly in the near to medium term: confidence is highest for CO_2 concentrations and then for temperature, but for C4 crops CO_2 fertilization benefits will be very limited (Long and Ort 2010), and temperature comes far behind moisture in determining plant production in warm, flat, water-limited regions. Contrastingly, high uncertainty subsists about the magnitude, timing and direction of future rainfall variability patterns, and precautionary adaptation strategies should embrace the full range of possible and (so far) equally probable moisture outcomes, including: increasing drought and excess humidity stresses, both incurred as a result of altered average conditions and of the possible increase in the frequency of extreme events (dry spells, floods); subsequent changing composition of crop pests, diseases, and associated biotic stresses; and concomitant risks of genetic erosion.

More projected variability calls for more versatile systems and flexible germplasm that perform satisfactorily under a wider range of climatic conditions, rather than excel in a narrow subset of conditions (Nelson et al. 2009). This is particularly relevant because variability remains unpredictable for smallholder systems. With such high uncertainty on climate outcomes, adaptive breeding for West Africa may therefore consider:

- *The persistence of existing variability modes,* especially on high and medium frequencies, and the need to maintain and when necessary restore or enhance adaptation to these. There is no such thing as "normal rainfall" in the West African region (Hulme, 2001), nor has any significant change in the magnitude of inter-annual variability been measured. Natural variability in inter-annual rainfall has always been extremely high, effectively masking effects of multi-decadal cycles and hence likely to also mask effects of anthropogenic climate change. For example, an ICRISAT project site in the Maradi region of Niger received 198 mm rain in the year 2009 but 680 mm in 2010 (Traoré et al. 2011). The beginning of the rainy season is usually very variable and unpredictable while the end of the season, particularly in the Sudanian and Northern Guinean zones, is slightly more stable (Vaksmann et al. 1996). Droughts, floods and excessive rainfall have always been common experiences for West African farmers. Ensuring continued adaptation of new germplasm to the inter-annual variability in the structure of rains should receive highest priority to preserve system resilience and avoid unnecessary strain in preparation for the longer term (Washington et al. 2006). Similarities in the uncertainty structure of rainfall indicator distributions on the short and long term may allow easy portability of adaptation traits across timescales. A second priority would be for breeding programs to anticipate and better synchronize their selection-release cycles with the natural multi-decadal fluctuations of West Africa's moisture regimes.

- *Interactions between climate and other drivers of change,* as climate does not operate in a vacuum (Vogel 2005). Other more powerful and predictable drivers of change provide important clues for prioritization of breeding targets. Intensification objectives associated with population growth will require higher water use efficiency. Independently and concurrently, in these semi-arid and sub-humid regions, population growth is largely associated with a decrease in average plant available water due to cropland expansion onto marginal soils. This predictable, rapid trend may explain why certain cultivars developed for drier climate conditions (following droughts of the 1970-80s) are nevertheless adopted today in spite of the ongoing rainfall recovery. It will be important to prepare for the next multi-decadal desiccation phase, which may start as early as 2020 under unprecedented high population pressure.

- *Limitations in the applicability of the space-time analogue approach:* Warming and cooling patterns in the coupled atmosphere-ocean system have historically translated into poleward (e.g. Holocene hypsithermal; 1990s-present) or equatorward (e.g. Holocene neoglacial; 1970-80s) migrations of agro-climatic zones. Similar patterns are anticipated for the future (Kurukulasuriya and Mendelsohn, 2008). Relying on "analogue locations" that have *today* the climatic characteristics that are expected *tomorrow* in a target production zone (CCAFS 2011; ICRISAT 2011; Burke et al. 2009) can help predict the effect of changing climate on crops. However this approach is more suited to (predictable) temperature than (unpredictable) rainfall patterns and gradients, which in West Africa are associated with strong plant photoperiod sensitivity as a specific adaptation mechanism to rainfall variability. Photoperiod sensitivity which determines adaptation to latitude (Craufurd et al., 1999) will constrain meridional (i.e. North-South and South-North) movement of elite cultivars under climate change. Therefore, there is no straightforward way to trade space for time to predict climate change effects on crops in West Africa.

- *Enhanced climate proofing in breeding trials:* due to short project lifecycles, the time coverage of breeding activities is, more often than not, a non-representative sample of the typical climate conditions and specifically, variability experienced by smallholders in the Tropics, rising concern among some donors (Roger Stern, personal communication). Likewise, resource constraints severely limit the number of trial locations relative to the enormous diversity of targeted environments, perpetuating a deceiving myth of climatic homogeneity across a region indiscriminately referred to as "the Sahel" by scientists and policy makers alike. While this problem of space-time representativeness can be partly addressed in a participatory breeding and selection approach (e.g. with farmers helping scientists contextualize a given trial performance using their indigenous knowledge of local climate), it cannot realistically be solved by breeding alone: the sample of target environments can only be dramatically augmented through computer simulations, requiring close collaboration among breeders, farmers, and crop modelers (breeding *in silico*).

Mechanisms of adaptation to climate variability

Cooper et al. (2008) showed for sites in Eastern and Southern Africa that the lower the average total rainfall of a site, the higher the rainfall variability. So the most vulnerable farmers are often hit hardest by climate variability. Without effective intervention, projected increases in climate variability can be expected to intensify the cycle of poverty, natural resource degradation, vulnerability and dependence on external assistance (Jarvis et al. 2011). A better understanding of the mechanisms of coping with current climate variability is therefore essential, and is a prerequisite for adaptation to future climate change (Cooper et al. 2008). Yield stability in unpredictably variable environments can be achieved through:

(i) Phenotypic plasticity ("individual buffering"): individual plants showing a plastic response to variable environmental conditions, e.g. low tillering in stress conditions and higher tillering in more favorable years or when conditions improve (more examples will be given below); and

(ii) Diversity for adaptation traits in a genetically heterogeneous variety or plant stand ("population buffering", Allard and Bradshaw 1964): e.g. if individual plants in a field differ for flowering dates by one month, a two-week drought during the flowering period would not hit all plants in their most sensitive stage. Some early flowering plants would have escaped and other late flowering plants would still be in the less sensitive vegetative stage. This will assure that at least some grain will be produced.

(iii) Traits directly conferring tolerance or resistance to abiotic- and biotic stresses that occur due to climatic variation or climatic extremes.

The first two mechanisms were defined by Lerner (1954) as developmental and genetic homeostasis. These mechanisms also refer to different yield stability concepts – static *versus* dynamic- as defined by Becker and Léon (1988) and Annicchiarico (2002). Population buffering results in a more static stability – the plant population producing a stable minimum yield but no clear response to better years, because in every year, only a certain percentage of all plants will be best adapted to the prevailing conditions. Response to favorable years (dynamic stability concept) is better achieved via phenotypic plasticity or individual buffering. The target farmers' risk aversion needs to be considered to guide selection. A high minimum yield, i.e. grain yield under the most adverse conditions, tends to be more important for vulnerable smallholder farmers than high cultivar response in more favorable years, as was documented for pearl millet in dry Western Rajasthan in India (Van Oosterom et al. 1996; Weltzien et al. 1998).

Useful practices include, e.g. the relative weights given to yield or performance under stressed conditions *versus* under favorable conditions, when making selection decisions. Use of simple means across environments may not be recommendable as these generally give greater weight to performance in the highest yielding-, most favorable, environments. One option to avoid this is to use standardized values (mean of 0 and standard deviation of 1) instead of genotype means for selection decisions. The use of selection indices would further enable consideration of both the relative importance of specific environments or traits as well as the confidence (repeatability) of results from each environment. Capturing the relative importance of specific traits or results from specific environments can be achieved by using economic weights to multiply observed values. Heritability estimates (or repeatabilities) can be used as weights to give greater emphasis to the more reliable results by multiplying observed values by their respective heritability estimates.

The role of the genetic structure of the cultivar

The genetic structure of a variety influences the variety's potential to express individual and population buffering for adaptation to climate variability. The development of heterozygous and/or heterogeneous cultivars is therefore one option to enhance the cultivar's capacity for buffering against climate variability.

Developing heterozygous cultivar types

Individual buffering may be enhanced through heterozygosity (two different alleles at a gene locus) or alloploidy (different alleles available from the different genomes of an alloploid species, e.g., wheat) (Schnell and Becker 1986; Feldman et al. 1986). Such intra-genotypic diversity can enlarge the adaptation range of a genotype because of allele

and concomitant enzyme diversity – and therefore its potentially better adaptation to climate variability. The degree of heterozygosity can be influenced by breeders through:

(i) choice of variety type – hybrids, synthetics, and open-pollinated cultivars of outcrossing species like pearl millet posses high levels of heterozygosity;

(ii) exploitation of heterotic groups in both population and hybrid breeding to maximize heterozygosity in these types of cultivar;

(iii) recurrent selection for increased outcrossing rate in predominantly autogamous species (e.g. sorghum).

A number of studies have shown the benefits of heterozygosity and hybrid vigor in pearl millet and sorghum in Africa (e.g., Ouendeba et al. 1993, Haussmann et al. 1998, 2000; Haussmann 2009; ICRISAT 2009, Rattunde and Diallo 2009). Haussmann (2009) showed that pearl millet population hybrids with significant superiority over the parental populations can be obtained *via* crossing of genetically distinct landraces from West Africa. Population hybrids could be regrown by farmers, and might therefore be a good option in areas where commercial seed systems are not yet developed. Guinea-race sorghum hybrids have shown promising performance in the Sudanian zone of West Africa (Rattunde and Diallo 2009). Parzies et al. (2011) reported significant progress for increased outcrossing rate in Caudatum-race sorghums from Sudan using marker-assisted selection.

Developing heterogeneous cultivar types

Population buffering requires intra-varietal genetic variation for adaptive traits. Haussmann et al. (2007) studied intra-varietal heterogeneity of flowering time in six pearl millet landraces from Niger. Genetic differences between the earliest and the latest full-sib family derived from the same landrace were 16 days at minimum (Bondabia landrace) and 39 days at maximum (Bazagome landrace). The enormous intra-varietal

heterogeneity in these Sahelian pearl millet landraces for flowering time likely reflects adaptive benefits of this intra-population diversity, whereby only a portion of plants is at their most sensitive stage at any point in time (Haussmann et al. 2007). This diversity arose through natural and farmer selection over many generations, and is likely an important mechanism for adaptation to high inter-annual climate variability in the Sahel. Sahelian pearl millet breeders are thus faced with the question of how much intra-varietal heterogeneity is desirable, or necessary, to obtain improved and stable varieties that consistently out-yield local cultivars under extremely variable growing conditions. This may be in conflict with the common understanding that "improved" cultivars should be distinct, uniform and stable.

Genetically heterogeneous cultivar types that can profit from population buffering include varietal mixtures, multi-line varieties (autogamous species, but components should be specifically selected for complementary traits), open-pollinated population and synthetic varieties, as well as 3-way, 4-way and top cross hybrids. Additionally, use of a bulking method of generation advance during inbreeding of predominantly self-pollinated species can be used to maintain uniformity for key agronomic traits such as plant height or grain color, but retain genetic diversity at many other loci. The resulting diversity may or may not be visible, but could contribute to population buffering if alternative physiological pathways are retained.

Breeders seeking to exploit population buffering for flowering would need to maintain varietal identity for other traits such as panicle and leaf characteristics. Line and single-cross hybrid cultivars are genetically uniform and thus would not express population buffering. Such highly uniform variety types should be avoided by breeders aiming to improve adaptation to extreme climate variability (where individual buffering mechanisms may be insufficient), unless farmers can use multiple varieties differing for key adaptation traits, like flowering time. The use of multiple varieties by farmers, and

the habit to change varieties cultivated in response to specific weather patterns is a common feature of sorghum cultivation in the Sudanian zone of West-Africa (Siart et al. 2008). In the Sahelian areas, farmers often grow mixtures of very diverse sorghum types, even including different races.

Selection methods and traits for adaptation to climate variability

Indirect versus direct selection

Selection methods targeting adaptation to climate variability can be divided into *direct selection* for performance in the target stress environments and *indirect selection* methods for e.g., specific morphological, phenological or physiological characteristics under stress or under non-stress conditions. Quantitative-genetic selection theory has shown that indirect selection can only be effective if the indirect (physiological/ morphological/ phenological) trait is easy, cheap and fast to measure (allowing for a higher selection intensity) and if there is a strong positive genetic correlation between the indirect selection trait and yield performance under stress (Falconer 1989). For example, selection for adaptation to highly variable onset of rains (sowing dates) could be done directly by conducting multi-location, multi-year trials to sample a range of sowing dates for evaluating yield performance. In contrast, evaluation of photoperiod sensitivity could be conducted to indirectly select lines expected to have more stable performance over varied sowing dates (Curtis 1968). In fact, the strong relation between later maturity and photoperiod sensitivity in sorghum enables observation of flowering in a single early sowing date to indirectly measure photoperiod sensitivity (Clerget et al. 2007).

However, environmental stresses such as drought may not actually be a single phenomenon but rather a complex. For example, drought occurrence during seedling establishment, panicle formation, flowering or grain filling can represent totally different physiological challenges and require distinct genetic resistances. Therefore selection for

resistance to a complex stress such as drought, for example, is always a type of indirect selection. Thus the more precisely the stress can be defined, the higher should be the correlation with the target and the larger the expected gains from selection.

Traits for adaptation to climate variability

According to our experience, a number of specific traits may be targeted to improve adaptation of pearl millet and sorghum to climate variability (Table 1). These are generally traits that enhance phenotypic plasticity and/or tolerance to particular stresses prevalent in the West African region. However one needs to bear in mind, that adding additional traits to a selection protocol reduces the selection intensity, and thus expected gain for yield performance, unless the indirect selection criterion targets yielding ability under stress conditions.

Photoperiod-sensitive flowering of West African guinea-race sorghum and pearl millet landraces is one example for a trait conferring phenotypic plasticity or individual buffering. Photoperiod-sensitivity enables flowering to occur at a more fixed calendar date despite highly variable planting dates. Selection for extremely early maturity in the wake of drought periods in the 1970s and 1980s resulted in loss of photoperiodic sensitivity from much of the breeding material in pearl millet (Niangado 2001), as well as sorghum. However, a characterization of the photoperiodic responses of 424 West and Central African pearl millet landraces suggests that photoperiod sensitivity contributes to adaptation of a wide range of pearl millet germplasm, with 61% of tested materials showing significant responses (Haussmann et al. 2007). In the same study, long-cycle millets showed a stronger sensitivity to photoperiod than shorter-cycle cultivars. Photoperiod-sensitive flowering response is even more prevalent in Guinea-race sorghums which predominate in West Africa (Curtis 1968), and a similar strong relationship was reported between the duration of vegetative phase in an early sowing

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date and level of photoperiod sensitivity in sorghum (Clerget et al. 2007). The high frequency of photoperiod-sensitive flowering in local germplasm from West Africa underlines the adaptive value of this trait and therefore the importance of appropriately targeting this trait in cereal breeding for this region. To facilitate selection for appropriate photoperiodic response, allele-specific molecular markers are currently being identified in sorghum (Bhosale et al. 2011) and pearl millet (Bhosale and Parzies 2009).

High tillering potential is another example for individual buffering via phenotypic plasticity. Van Oosterom et al. (2005) showed that plastic tillering is a major adaptation trait enhancing dynamic yield stability of pearl millet in the dominant cropping system of harsh and extremely variable arid desert margins of western Rajasthan (India).

Earlier maturity may also help adaptation to increased frequencies of terminal drought resulting from climate variability and change. Vigouroux et al. 2011 analyzed flowering time in a representative sample of pearl millet landraces from all over Niger in the same villages in 1976 and 2003. Compared to the 1976 samples, samples collected in 2003 displayed a shorter lifecycle, and a reduction in plant and spike size. Their genetic analysis also revealed that an early flowering allele at the PHYC locus increased in frequency between 1976 and 2003. The increase exceeded the effect of drift and sampling, suggesting a direct effect of selection for earliness on this gene. They concluded that recurrent drought lead to selection for earlier flowering in these pearl millet landraces from Niger. Regarding extra early maturity for drought escape in predictably short growing periods, it must be underlined there is always an optimal range of flowering time for each site beyond which cultivars are not adapted; growing extra early varieties in regions where they are not adapted can cause other problems such as bird damage and multiplication of pests or grain mold and sprouting before harvest.

Additional traits we expect can play an important role in adaptation to climate variability include (Table 1):

- flooding tolerance for survival in inundated fields: this trait is especially important for sorghum grown in heavier soils or depressions;

- seedling heat and drought tolerance for better survival of early season heat waves and drought periods: a trait of high importance in the Sahel where some farmers tend to replant several times until their field is established; and

- phosphorus efficiency to reduce delay of flowering in low-fertility soils: low-P content in the soils is a major production constraint in West Africa whose interaction with drought stress is not yet well understood.

A better understanding is needed of the possible contributions of stay-green, drought-induced senescence, leaf area, and root architecture traits for adaptation to climate variability.

[Table 1 here]

Multiple environment testing and farmer-participatory breeding

Selection for climate variability adaptation will require testing/selection in many environments which enhances the chances of sampling key stress environments. On-farm testing is especially useful to obtain a critical mass of representative testing environments and production-system-relevant responses (Weltzien and Christinck 2008). For example, a one week earlier end of rains could have significantly more impact on a farmers' field where phosphorus deficiency delays development by up to two weeks relative to well fertilized research station fields.

Multi-location replicated variety yield trials have been conducted in approximately 30 farmer-managed sites per year in the major sorghum production zone in Mali over the past decade. These trials, involving farmers in the various steps of variety evaluation, have resulted in the identification and release of sorghum varieties and hybrids that

perform consistently better than local varieties over the wide range of production conditions encountered in the Sudanian zone of Mali (Weltzien et al. 2008).

One example of farmer-participatory selection for adaptation to a specific stress by using selection opportunities presented by natural occurring stresses is the "Water-logging Resistant Sorghum Population in Mali, West Africa" (Rattunde et al. 2009). The field where a random-mating sorghum population was grown was flooded for three weeks due to unusually heavy rains. Selections from the more desirable plants that survived that year most likely possessed some tolerance to water logging as the entire field was flooded. The same year farmers expressed interest in having a sorghum variety for fields that tend to be inundated in years of heavy rainfall. The following year this "water-logged" cycle bulk was given to two farmers in different villages who sowed it in low-lying fields. One farmer selected panicles within it for use as seed the following year. The next year the population performed exceptionally well in inundated fields and many neighbors, especially women with low-lying fields, requested seed of the flooding resistant "variety".

Genomic selection

The enhanced understanding of gene functions in relation to stress tolerance and continual reduction of DNA marker costs makes genomic selection a promising strategy to improve abiotic and biotic stress resistance (Heffner et al. 2009; Jannink et al. 2010). Genomic selection uses high-density DNA marker information to predict performance. This approach seems more suitable for improvement of quantitative traits determined by many genes with small effects than classical marker-assisted selection targeting individual quantitative gene loci. Albrecht et al. (2011) could show that models including genomic information in prediction of maize testcross performance yielded significantly higher prediction accuracies than models based on pedigree information alone. According

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to our present knowledge, no results are yet available from genomic selection for sorghum and pearl millet.

Long-term development of adapted diversity using a dynamic genepool management approach

Suitable genetic variation and availability of sources of resistance to specific production constraints is the capital of any breeder. Without suitable genetic variability, no gain from selection can be made. Developing adapted diversity for sustainable breeding progress is a specific long-term task that should not be neglected by breeders.

Dynamic gene-pool management in combination with farmer-participatory population improvement (Figure 1) seeks to produce long-term genetic improvement of diversified populations to better meet farmer's needs for varietal adaptation to variable and changing climates as well as for site-specific requirements (Simmonds 1993; Haussmann et al. 2004; Enjalbert et al. 2011). The dynamic genepool approach used in pearl millet and sorghum improvement programs in West Africa uses the varietal diversity available within each major agro-ecological zone to create new broad-based populations through crossing and recombination of genetically and/or geographically diverse genetic materials selected by farmers and breeders (Vom Brocke et al. 2008). Seed lots of the base-population are distributed to farmers in contrasting sites of a target region. The ensuing natural- and recurrent selection by farmers and/or breeders on the population grow-outs lead to development of new subpopulations. These subpopulations can provide excellent sources of variation for specific adaptive traits in acceptable genetic backgrounds, with farmers' priority agronomic-, quality- and adaptive traits. The population approach also provides new trait combinations through the periodic recombination of selected materials. The sum of all subpopulations grown in the contrasting sites can be considered as "mass reservoir of genetic adaptability" (Simmonds

1993; Haussmann et al. 2004). The sub-populations can then be used for development of contrasting varieties with differing adaptive characteristics. As such, this gene-pool approach enables creative management and use of genetic diversity to "offer a wide diversity of material to the wide diversity of farmers" (Weltzien et al. 2000). The above-mentioned success story about the "Water-logging Resistant Sorghum Population in Mali, West Africa" (Rattunde et al. 2009) gives one example output of the dynamic genepool management approach. Haffke (2010) showed that after two selection cycles, certain farmer-selected pearl millet populations were able to out-yield local varieties and improved checks under on-farm conditions.

In out-crossing species such as pearl millet, care must be taken to isolate sub-populations or to grow them in larger fields where the center would be harvested as seed. Otherwise the adaptation of the sub-population maybe diluted by surrounding, less well adapted varieties.

In addition to facilitating applied breeding efforts, the dynamic genepool management approach can also further *in-situ* conservation of plant genetic resources (Enjalbert et al. 2011). An important expectation of *in-situ* genetic resource management is that conserved materials maintain good adaptation despite environmental changes, especially if these changes are consistent and directional, favoring effective response to selection pressures. In the case of high inter-annual climate variability, the divergent selection pressures can result in enhanced intra-population heterogeneity for adaptation traits. Contrastingly, germplasm conserved *ex-situ* in genebanks remains static under the best of expectations.

Enhancing population buffering via system's diversification

West African sorghum and pearl millet farmers frequently cultivate several different varieties in the same season. These varieties are often contrasting for maturity. Sorghum

farmers in the Sudanian zone of Mali choose diverse varieties for sowing, with individual farmers often growing two to four different varieties. At a village level the diversity is still greater, with generally ten to 25 different varieties cultivated in a given season (Lacy et al. 2006; Siart et al. 2008). Farmers' strategy of using varietal diversity aims to optimize their whole farm production given their predictions of local climate conditions and their various production conditions and objectives.

Various types of intercropping of different species are also practiced that can provide a type of population buffering. Intercropping of cereals with legumes (e.g. pearl millet/cowpea, sorghum/groundnut) is very common. These intercrops can also provide benefits for soil nutrient availability and control of the parasitic weed *Striga* (Carsky et al. 1994; Van Mourik et al. 2008), effects which could enhance resilience to climate variability. Intercropping of different cereal crops is also common in West Africa (pearl millet-sorghum, maize-sorghum), generally with the first crop earlier maturing than the latter. These intercrops can possibly increase the effective use of water and soil resources, reducing vulnerability and enhancing production stability. Well-designed intercropping systems can also help weed management and protect soils from erosion after heavy rainfall, but competition for soil moisture among the intercropped varieties must be minimized.

Thus it is not surprising that the farmers in the drier, more climatically unpredictable Sahelian zone extensively practice intercropping. In the Thar Desert of Rajasthan, farmers intercrop pearl millet with five to ten or more other species. In contrast, farmers in the higher rainfall zones in both the Indian subcontinent and the Sudanian and Guinean zones of West Africa extensively cultivate sole crops or at most intercrop of only two species, often with the cereal heavily predominating over the associated legume species.

The use of varietal diversity as well as intercropping options leads to systems diversification on farm- and landscape levels that can maximize production outputs of a whole region. Further, such production system diversification will be required for adaptation to more severe climate change (Howden et al. 2007)

Developing cultivars with specific adaptation to natural resource management (NRM) techniques

Crop improvement alone cannot produce miracles. The development of new improved and climate-proof cultivars must go hand in hand with sustainable soil fertility management and water conservation and drainage techniques. Integrated genetic and natural resource management (IGNRM, Twomlow et al. 2008) combines improved production practices with varieties responsive to specific soil fertility and water conservation techniques. By avoiding the most common pitfalls of scientific reductionism, IGNRM provides a conceptual framework more representative of smallholders' holistic management of the cropping system. Within that framework, analyses of genotype $\times$ crop management $\times$ location (environment) interactions can help identify synergistic combinations of crop management and variety options that surpass the individual impacts of each technology.

The breeder's contributions to IGNRM strategies for adaptation to climate variability may include:

- Developing genotypes suitable for mixed cropping systems; for example pearl millet and cowpea cultivars with complementary maturities, plant and rooting architectures that maximize total value of production and enhance stability in intercropping systems. As indicated above, this can reduce the risk - if one crop fails due to early season drought, the other may still produce and profit from the gained space - and therefore

enhance the system's production stability. It may also reduce the overall workload as there may be spatial or temporal differences in resource use.

- Selective matchmaking of adaptation traits, or combinations thereof, with NRM; for example, photoperiod-sensitive cultivars may benefit more from water harvesting technologies such as contour ridge tillage (P. S. C. Traoré, unpublished data). This allows earlier planting and canopy development with higher final biomass yield, and yet avoids hastened maturity that penalizes harvest quality. It is best targeted to drier landscape positions and years (Traoré et al. 2004) and to dual-purpose crops (fodder + grain).

- Breeding for enhanced resource use efficiency; for example high phosphorous efficiency that maximizes economic benefit of improved nutrient management as well as reduces risks under deficiency conditions via increased crop root volume and reduced flowering delay and consequent terminal drought escape.

Costs of adaptation to climate variability

The costs of adaptation to climate variability may be manifold and are not yet well understood. Population buffering as mechanism of adaptation to unpredictable environmental heterogeneity means that in every year, a certain percentage of the plants in the field are not adapted and will yield below potential or even fail. To reduce this "yield cost", the genetic heterogeneity of a population may be optimized to fit best the climate variability at the location where the variety is grown. In the case of diversified cropping systems, enhancing precision of seasonal climate predictions and strengthening seed availability of diverse varieties would aid farmers in their tactical choices of crops and cultivars to maximize production in each cropping season.

Determining the costs of adaptation for specific traits would require information of the target population of environments and the frequencies of specific stresses. Photoperiod

sensitivity is one specific trait that would warrant further investigation in this line, with some evidence of non- or less-sensitive materials achieving higher grain yields in certain (non-stress) environments, whereas photoperiod-sensitive varieties would have lower but more stable yield over a range of (variable) environments (Benoit Clerget, personal communication). For this trait, and especially in the context of West African sorghums, it is also very important to consider not just grain yield in weight but in useable product, as even in cases where insensitive varieties could produce higher grain yields in weight, the actually useable product may be lower or zero due to insect, bird, or weathering-mold damage. Insensitive varieties with fixed vegetative period are at risk for these losses when sowing dates do not conform with the ideal date, whereas photoperiod-sensitive varieties can adjust their vegetative cycle to variable sowing dates, maintaining the time of flowering and maturity near the optimal date for quality grain and avoidance of threats such as birds and grain-mold/weathering. Photoperiod-sensitive flowering seems therefore to be a most valuable climate variability adaptation trait with relatively little costs of adaptation.

From a breeder's point of view, the required larger-scale, on-farm participatory testing that will enable assessments of varietal performance under evolving climatic variability causes additional costs. And, depending on the target environment, the more stress resistance traits need to be included in the selection, the lower will be the selection gains made for each individual trait, including yield.

Strengthening the adaptive capacities of farmers

Farmers have developed and practiced an array of strategies for adaptation to variable climate, e.g. creating and maintaining a diversity of landrace varieties, using early and late varieties in their production systems, intercropping cereals with legumes, staggered planting dates, etc. The suggested strategies such as breeding genetically heterogeneous

cultivars and maintaining appropriate photoperiod-sensitive flowering at least partially build on farmer's local knowledge and are therefore expected to be socially acceptable. For researchers and development personnel to most effectively contribute to farmers' evolving strategies, it is necessary that these strategies and the constraints and opportunities for their use are understood as fully as possible. On the basis of this knowledge, the development of new variety and crop management options that will diversify options available to farmers and enhance their adaptive strategies can be pursued.

Farmer's input into the different stages of a breeding program will be vital for effective development of new climate-robust varieties that possess the required array of agronomic, quality and adaptive traits. This input can help assure effective priority setting, identification of parental materials, selection and testing and dissemination activities. Using such an approach will assure that selected materials correspond to farmers' needs and preferences and speed adoption by farmers (Christinck et al. 2005).

Key elements for enhancing farmers' capacity to contribute to- and benefit from research and development undertakings include the following:

- Enhanced access to new improved varieties and ability to maintain them; this may require strengthening of community-based quality seed production of the range of crops and cultivars that show specific adaptation to a community's environment;

- effective communication methods for linking farmers and development actors, facilitating two-way information flows in ways that are mutually comprehensible;

- enhanced capacity to test new varieties and crop management practices under their conditions.

The "Opposite Pyramid Approach" (Herrmann et al. 2010) developed within the CODEWA project (http://codewa-icrisat.uni-hohenheim.de/) is one approach based on participatory action research for rapid but sustainable introduction of options for varietal

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diversification. The Opposite Pyramid Approach begins by evaluating a relatively large number of diverse cultivars, for example 32, in on-farm, small-plot, researcher-managed trials. Based on farmer's trial evaluations, farmer-managed on-farm trials are conducted in the second and third year with reduced number of varieties and increased plot size per variety to minimize soil micro-variability effects, and to identify adapted and farmer-preferred variety options. In the third year, training of farmers on community-based varietal maintenance and seed production techniques is initiated to assure durability of the diversification effort, especially for out-crossing species (Herrmann et al. 2010).

Similarly, the Malian national sorghum improvement program together with ICRISAT is implementing a two stage farmer-participatory variety evaluation program. The first stage involves larger 32-entry trials that are conducted in eight to ten villages over two years. The most promising varieties, identified by farmers with benefit of researchers' multi-location statistical yield analyses, then proceed to smaller, strictly farmer-managed, 2-5-entry trials in more than 300 villages for large-scale adaptation and farmer preference testing (Weltzien et al. 2007; Weltzien et al. 2008). This approach gives farmers the opportunity to continuously test and identify new options for their variety portfolio, while simultaneously providing researchers with feedback on preferred traits and farmers' needs. Furthermore, this approach enables local seed cooperatives to regularly choose new varieties for seed production and commercialization, and thus stay in business.

[Table 2 here]

Conclusions

A wide range of crop improvement options for enhancing adaptation to climate variability are available (Table 2). These include the choice of the type of cultivar (degree

of heterozygosity and heterogeneity), direct selection in multiple environments, including farmer-participatory testing, indirect selection for individual adaptation traits using conventional or genomic selection methods, a dynamic genepool management approach, and selection for responsiveness or compatibility to improved crop and soil management techniques. To maximize impact, several options need to be combined. A better knowledge of the target environments and seasonal predictions may reduce the potential costs of adaptation. Furthermore, seed systems need to be strengthened so that they effectively provide access to new varieties and a diverse range of varieties that respond to farmers' current and evolving needs, including adaptation to variable and changing climatic conditions.

Acknowledgements

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List of figures and tables

Fig. 1 Dynamic genepool management – an option for *in-situ* management of plant genetic resources for climate change adaptation

Table 1 Traits of potential use for applied breeding targeting adaptation to climate variability

Table 2 Crop improvement options for enhancing adaptation to variable climates

Table 1 Traits of potential use for applied breeding targeting adaptation to climate variability

Trait	Contribution	Importance for	
		P. Millet	**Sorghum**
Photoperiod sensitivity	Matching vegetative cycle to available growing period despite variable sowing dates; reduce risks of biotic (damage by birds, grain molds) and abiotic (terminal drought) stress due to variable sowing dates	X	XX
Plastic tillering	Spread of flowering/maturity period, reduce exposure to severe stress at a single point in time; capacity to respond to improved conditions	X	X
Very early maturity	Complete grain filling in more predictably short growing period	XX	X
Flooding tolerance	Plant survival under temporary flooding	X	X
Seedling heat and drought tolerance	Survival of small seedlings, physiological efficiency under higher temperature conditions	X	
Phosphorous (P) efficiency	Less delay in flowering/maturity under limited P availability, reduce risks of poor grain filling, reducing midge attacks in sorghum	?	?
Leaf width/area	Narrower leaves may be advantageous under hotter and drier conditions, as observed with landrace millet varieties in Rajasthan, India	X	
Stay Green	Grain filling under terminal drought may be favored with continued photosynthetic activity	?	?
Drought-induced senescence	Minimize plant evaporative loss of water, extending physiologically active period under/after drought	?	?
Root architecture	Volume and zone of soil exploited for water and nutrient uptake	?	?

X, XX: moderately important and very important, respectively;

? Requires more investigations to prove usefulness in West Africa.

Table 2 Crop improvement options for enhancing adaptation to variable climates

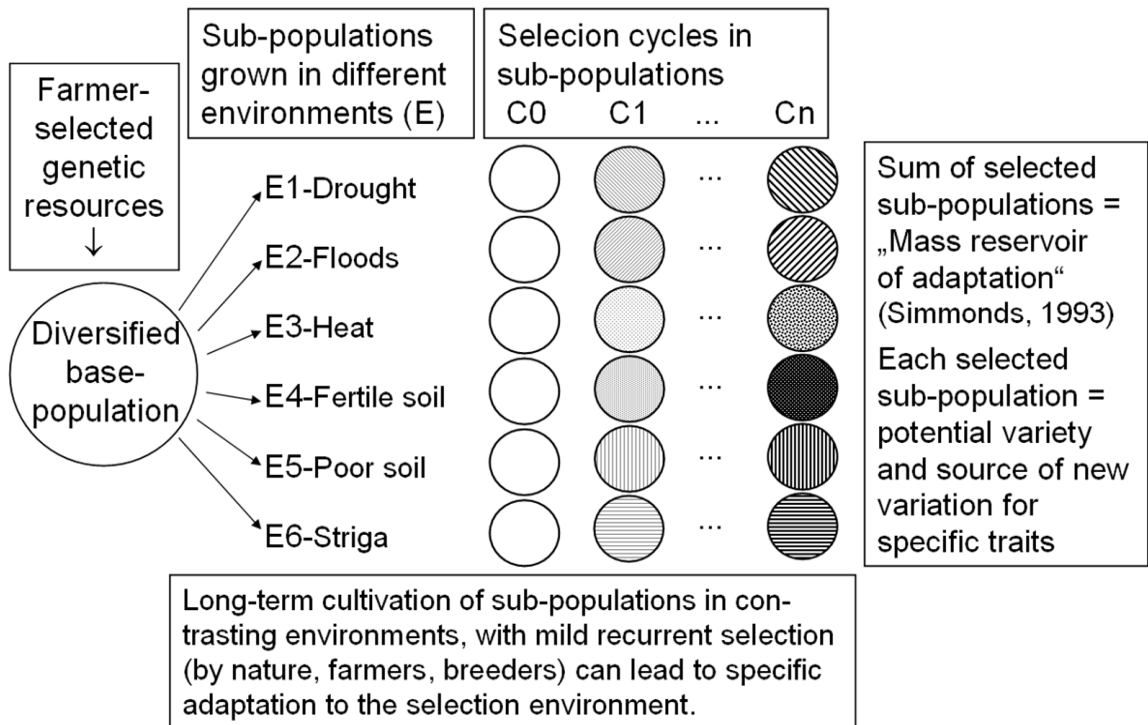| Option	Contribution
Developing heterozygous cultivar types (open-pollinated varieties, hybrids, selection for high outcrossing rate)	Opportunity to benefit from heterozygosity for individual buffering
Developing heterogeneous cultivar types	Opportunity to benefit from heterogeneity for adaptation traits such as flowering date for population buffering
Direct selection for performance based on testing in multiple (very many) environments	Effective sampling of range of environments; increase opportunity of assessing progeny response in specific "stress" conditions (e.g. late-sowing, droughty/flooded), allows to assess phenotypic plasticity
Direct selection for performance and farmer preference based on farmer-participatory testing	Opportunity to assess farmer and genotype response to climate variation and impact of climate variation in actual production systems
Indirect selection for adaptation based on selection for traits expected to provide adaptive benefits	For list of target traits, see Table 1. Relative contribution to adaptation depends on genetic correlation of traits with yield performance in variable environments
Indirect selection in stress nurseries managed for specific environmental conditions	Increased control of stress factor(s) in degree, timing and uniformity, resulting in higher repeatability and better discrimination among genotypes; relative contribution depends on frequency of specific stress in the target population of environments
Population / genepool management in target stress environments	Selection for specific adaptation to the stress factor; in case of highly variable environment: divergent selection results in maintenance of optimal degree of genetic heterogeneity for adaptation traits
Marker-assisted and genomic selection	Potentially more efficient selection for traits controlled by few gene loci with large effects
Development of varieties with specific adaptation to specific crop management techniques	More efficient/effective resource use, maximize total (value of) productivity and reduce risks, synergies with mutually enhanced benefits of improved varietal and management technologies

The Concept of Dynamic Genepool Management

Fig. 1