Mechanisms of adaptation to climate variability in West African pearl millet landraces – a preliminary assessment

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Introduction

Landraces are generally expected to possess specific mechanisms of adaptation to their growing environments. In West and Central Africa (WCA), growing conditions of pearl millet (Pennisetum glaucum) are characterized, among other hazards, by highly variable beginnings and endings of the rainy season, and unpredictable drought stress at any time during the growing season. Adaptation to such unpredictable variable environment can be due to individual and/or populational buffering (Allard and Bradshaw 1964), two mechanisms initially defined by Lerner (1954) as developmental and genetic homeostasis. Individual buffering may be favored by phenotypic plasticity. Photoperiod-sensitive flowering is an example of phenotypic plasticity that can enhance adaptation to variable planting dates followed due to a scattered beginning of the rainy season in a region, as typical for WCA. It enhances simultaneous flowering of the cultivar in the target region, independent of the individual date of planting in different fields. This has particular advantages in terms of reducing bird damage and insect pressure; prolonging vegetative development in case of early planting but accelerating development in case of late planting; therefore fitting plant development to available rainfall patterns and resulting potentially in increased yielding stability. Populational buffering can be promoted by genetic heterogeneity in plant stand as different genotypes present in the population are specifically adapted to different environmental conditions (Bradshaw 1965). An example is intra-varietal variation for flowering time, which would assure that in case of a dry spell, not all plants in the field will be affected by drought in their most sensitive flowering stage.

The objectives of the present study were to: (1) investigate preliminarily the importance of photoperiod-sensitive flowering; and (2) describe the variability of flowering time in WCA pearl millet landraces – two mechanisms of adaptation to climate variability with potential implications for present and future breeding programs in WCA.

Materials and methods

Photoperiodic response of WCA pearl millet landraces. In total, 424 pearl millet landraces from all over WCA were planted in Sadoré, Niger (13°06' N, 2°21' E) on 14 July and 15 August 2006. These relatively late planting dates were due to a late beginning of the rainy season in 2006. In the July plantings that served also as performance trials, the entries were divided into two groups: (1) 360 early-to-medium maturing entries, randomized as a design with 45 incomplete blocks per replication, 8 plots per incomplete block and 3 replications, and (2) 64 late maturing accessions randomized in an $8 \times$ 8 lattice design with 3 replications. In both trials, plot size consisted of two rows of 4.8 m length, with 0.75 m interrow distance and 0.8 m distance between hills within a row (7 hills per row). The August planting was an unreplicated observation nursery with 1-row plots of 7 hills, and the same spacing as above. The August planting was irrigated weekly with 30 mm to avoid drought stress. Thinning was done to two plants per hill in both planting dates. Photoperiodic response was measured as change in cycle length in the August versus July planting. Highly negative values mean a sharp shortening of the cycle in the cultivar, and therefore, a photoperiod-sensitive reaction; values not significantly different from zero mean insensitive; values largely above zero indicate a special reaction, which may require further validation.

Variability of flowering time within WCA pearl millet landraces. Within the frame of a recurrent selection program, full-sib families (FSF) derived from six pearl millet landraces from Niger were grown in 2005 and 2006 at the ICRISAT station in Sadoré, Niger (Table 1). Each plot consisted of one row of 3.2 to 4.8 m length (dependent on the trial), with 0.75 m interrow spacing, 0.8 m intra-row spacing and thinning done to two plants per hill. Different traits were assessed in the trials, but only time to 50% flowering is considered here. Repeatabilities of a plot value (%) were estimated as: 100*Vg / (Vg + effective error variance), with Vg being

Original landrace			Time to 50% flowering			
	Test year	No. of FSF studied	Mean of all FSF (days)	Range among the FSF (days)	Repeatability (%)	Duration of flowering period (days)
Bazagome	2005	100	64	57–96	85	39
Bodenji	2005	121	66	58-76	75	18
Kolala	2006	68	64	55-75	54	20
Darankoba	2006	96	69	60-81	43	21
Bondabia	2006	87	70	62-78	71	16
Adarankoba	2006	80	74	56-84	62	28

 Table 1. Mean, range and repeatability estimates for flowering time, and duration of the flowering period for full-sib families

 (FSF) derived from six pearl millet landraces from Niger, tested at ICRISAT, Sadoré, Niger.

the treatment variance component (Utz 2007). The PLABSTAT software (Utz 2007) was used for statistical analysis.

Results and discussion

Photoperiodic response of WCA pearl millet landraces. Time to 50% flowering of the landraces differed significantly and ranged from 43 to 109 days in the July planting, revealing a large diversity for flowering date in the landrace collection. Across 417 entries (7 missing values), the photoperiodic response, ie, the change in cycle length in the August compared to the July planting was approximately normally distributed with a mean of minus 8.7 and a range from minus 28 (sharp shortening of the cycle) to plus 22 days (prolongation of the cycle). A fraction of 61% (258 out of 417 landraces) could be classified as photoperiod-sensitive; the remaining 39% (159 landraces) did not differ significantly from zero change in cycle length or actually prolonged their cycle, a phenomenon that was surprising and may require further investigation. The extent of photoperiod sensitivity was correlated to flowering date of the landraces in the July planting (coefficient of correlation r = -0.71, P =0.01), indicating that late varieties tended to be more photoperiod-sensitive than early cultivars. This seems to make sense as it may biologically not be possible to shorten the cycle below a certain minimum period.

Variability of flowering time within WCA pearl millet landraces. All six sets of FSF revealed highly significant variation for flowering time (Table 1). Differences between the earliest and the latest FSF were 16 days at minimum (in Bondabia landrace) and 39 days at maximum (in Bazagome). High repeatability estimates for flowering time point to the genetic origin of this observed variation.

Implications for pearl millet breeding in WCA. It may not be just by chance that WCA pearl millet landraces are actually displaying both individual and populational buffering mechanisms against environmental variability. The present study suggests that both photoperiodsensitive flowering and intra-varietal heterogeneity for flowering time are traits that are present and important in a significant fraction of WCA pearl millet landraces. Assuming that these characteristics have evolved during thousands of years of natural and human selection, they must bear some advantage for survival and possibly grain yield performance and stability. Interestingly, both traits seem to act against each other, the photoperiodic sensitivity - enhancing uniformity for flowering, and intra-varietal heterogeneity for flowering time - enhancing variability of flowering dates. Deeper investigations are required to elucidate this phenomenon. There may be an optimum for both. A concomitant question the plant breeders are facing is: How much photoperiodism and genetic heterogeneity is most desirable, or necessary, in order to obtain improved, stable varieties that are actually able to out-yield local cultivars under extreme and variable growing conditions? The present study has shown that photoperiod-sensitive flowering seems to be more important in later flowering cultivars and less important in earlier cultivars, but this needs validation through a second-year experiment with the first planting date happening already in June, a more realistic scenario under WCA growing conditions. More experiments may also be required to clarify the role of intra-varietal diversity for adaptation traits like flowering date in yield stability and in reducing genotype × environment interactions. A better understanding of the mechanisms of coping with current climate variability will also be a prerequisite for adaptation to future climate change.

Acknowledgments. The authors thank A Abarchi, A Amadou, D Lankoande and H Garba for their excellent technical assistance. This study was funded by the Federal Ministry for Economic Cooperation and Development, Germany (photoperiodism trial), the International Fund for Agricultural Development (IFAD) and ICRISAT Core (FSF trials).

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