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Phosphorus uptake and utilization efficiency in West African pearl millet inbred lines

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ABSTRACT

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

Abbreviations: aVD, standardized average variance of a difference; CV_g, genetic coefficient of variation; BLUP, best linear unbiased predictor; BM, total above-ground biomass; FLO, days to flowering; GY, grain yield; HI, grain harvest index; HP, high phosphorus; HT, plant height; LP, low phosphorus; NL, number of leaves; NT, number of tillers; P, phosphorus; PBM, total P in biomass; PCBM, P concentration in biomass; PCG, P concentration in grain; PCS, P concentration in stover and/or shoots; PE, phosphorus efficiency; PG, total P in grain; PHI, P harvest index; PHI:HI, ratio of P harvest index to harvest index; PS total, P in stover and/or shoots; PUTE, P utilization efficiency; PWT, panicle weight; RDB, root dry biomass; r_g, genetic correlation; RS, root to shoot ratio; RSG, relative shoot growth; SD, stem diameter; SDB, shoot dry biomass; SV, seedling vigor; SWT, stover weight; w^2, repeatability estimates.

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1. Introduction

Low phosphorus (P) soils are a major constraint to crop production in West Africa (WA). Pearl millet, a staple crop in WA, is predominantly cultivated by small-holder farmers on low-input sandy soils, thus adaptation to those edaphic conditions is crucial for food security in this region (Shen et al., 2011). Fertilizer application rates are very low in WA with levels mostly below 5 kg P ha^{-1} (Obersteiner et al., 2013). Furthermore, most of the WA 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), hence most smallholder farmers' fields within WA have plant available P levels of the soil below the critical level of 7 mg P kg^{-1} soil (Manu et al., 1991; Doumbia et al., 2003). Enhancing phosphorus efficiency (PE) in pearl millet would offer an affordable option for improving yields in low-input farming systems (Ismail et al., 2007; Wissuwa et al., 2009; Rose et al., 2011) and would serve especially small-holder farmers in WA. PE can be defined as the ability to acquire nutrients from the soil and utilize them for biomass and/or grain yield production (Gerloff, 1977; Manske et al., 2000). It is therefore constituted by P uptake efficiency (ability to acquire P from the soil) and P utilization efficiency (the amount of biomass and/or grain yield produced per unit P in the plant), with the contribution of these two aspects of PE depending on crop species and environmental conditions (Manske et al., 2000; Rose et al., 2011; Wang et al., 2010).

Being an immobile element in the soil, P concentration in the soil solution is usually much less than 0.3 mg P L^{-1} and often as low as 0.001 mg P L^{-1} whereas concentrations in plant tissues could be as high as 300 mg P kg^{-1} (Bieleski, 1976; Manske et al., 2000). This makes the uptake of P from the soil very slow (Fitter and Hay, 2002; Hammond et al., 2004). P deficiency in the plant initiates a series of transcriptional, biochemical and physiological responses which either enhance the plant's ability to acquire P from the soil or improve the efficiency with which plants utilize P internally (Hammond and White, 2008). Such responses include the development of lateral roots and root hairs, as well as more dramatic root structures such as proteoid and dauciform roots, the secretion from roots of phosphatases and organic acids, and the induction of high-affinity and some low-affinity inorganic phosphate (Pi) transporters as well as establishing symbiotic associations with mycorrhizal fungi that aid P acquisition (Burleigh et al., 2002; Lambers et al., 2006; Ai et al., 2009; Fang et al., 2009; Yang and Finnegan, 2010).

Low-P tolerance in WA pearl millet has been studied mainly based on morpho-physiological attributes (Bationo et al., 1993; Buerkert et al., 2001; Brück et al., 2003; Faye et al., 2006; Beggi et al., unpublished) but most of these studies were only based on a few genotypes. Genetic variation has been reported for rooting parameters as well as fertilizer response in WA pearl millet (Manga and Saxena, 1988; Brück et al., 2003; Faye et al., 2006). Furthermore, Beggi et al. (unpublished) have shown genotypic differences for PE under pot trial conditions in WA pearl millet landrace varieties. The usefulness of morphological or physiological traits in a breeding programme depends on their genetic correlation with grain yield, extent of genetic variation, heritability, genotype-by-environment interactions and costs of assessment (Mir et al., 2012). According to Reynolds and Trethowan (2007), the use of such traits therefore requires proper definition in terms of stage of crop development at which they are relevant, the specific attributes of the target environment for which they are adaptive, and their potential contribution to yield. P availability has been shown to be critical in the early developmental stages (Barry and Miller, 1989; Rebafka et al., 1993; Hajabbasi and Schumacher, 1994; Plenet et al., 2000; Valluru et al., 2010) and therefore, P deficiency in early stages is a direct constraint for crop production, particularly under agricultural conditions where intensive soil fertilization is not affordable (Lynch, 1995; Calderon-Vazquez et al., 2008). PE can therefore be evaluated both at early and adult plant stages. Early growth stage evaluation would allow for the use of managed environment phenotyping which is thought to reduce environmental variability associated with field experiments thereby reducing the error variance and improving heritability and precision (Blum, 2011; Rebetzke et al., 2013). However, it is also accepted that in spite of the notorious heterogeneity in the fields, controlled experiments, especially under pot trial conditions, are usually far removed from the situation the plant would find itself in the field. This makes the results from controlled environments difficult to extrapolate to field conditions (Araus and Cairns, 2014) because the phenome is dynamic, conditional, with complex responses and a wide range of endogenous and exogenous signals integrated over the evolutionary and developmental life history of an individual (Houle et al., 2010; Cobb et al., 2013).

To date, no study has specifically focused on WA inbred lines as breeding materials and the genetic variation among them for several PE measures under pot and field conditions. Furthermore, information is lacking on the relationship between genotype performance at an early growth stage in pots and genotype performance of mature plants in the field. The objectives of the current study therefore were:

(i) to examine the genetic variation for low P tolerance related morphological traits, P uptake and P utilization efficiency in WA pearl millet inbred lines at an early growth stage in pot experiments and at maturity under field conditions under low and high P conditions;
(ii) to determine the relationships among the measured traits and grain yield from independent environments; and
(iii) to determine which traits show potential for use in indirect selection for grain yield under low-P.

2. Materials and methods

2.1. Genetic materials

One hundred and eighty inbred lines (IBLs) of pearl millet [*Pennisetum glaucum* (L.) R. Br. syn *Cenchrus americanus* (L.) Morrone] were developed from a collection of landraces from West and Central Africa to represent a large part of the diversity of pearl millet in this region, which is also the centre of origin for pearl millet. The list and details of the 160 inbred lines included in the field trials is shown in Supplementary Table 1. The inbred lines were at the fourth selfing generation (S_4) in the rainy season (RS) 2011 and the fifth selfing generation (S_5) in RS 2012. In the RS 2011, 180 inbred lines were evaluated in a pot experiment at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Sahelian Centre, Sadore, Niger. For the field experiments at a total of four locations, only 160 inbred lines among them could be included (due to seed shortage of some lines for field experiments owing to inbreeding depression). The same seed was used for both pot and field trials. In RS 2012, a subset of 52 contrasting genotypes were selected based on grain yield data from the four locations, and a second pot experiment was set up. No corresponding field trial was carried out in RS 2012.

2.2. Field trials

In the rainy season 2011, 160 inbred lines were evaluated at Sadore, Niger (17 36′ 28.04″N; 8 4′ 53.99″W) together with two checks in separate trials planted side by side under high