Genotype x environment interactions for grain yield of upland rice backcross lines in diverse hydrological environments

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Title: Genotype x environment (G x E) interactions were investigated in Vandana and a subset of 13 BC2 and BC3 lines of an improved indica upland rice cultivar, Vandana, backcrossed with a drought-tolerant japonica cultivar, Moroberrekin, which has a thick and extensive root system, in response to eight hydrological field environments conducted in Los Banos, in the Philippines, between 2001 to 2003. The G x E interaction accounted for 13% of the total sum of squares with environment and genotype responsible for 84% and 3%, respectively. Cluster analysis identified four environment and six genotype groups, which accounted for 70% of the GxE sum of squares. Of this, AX1, AX2 and AX3 accounted for 27, 22 and 21% of the GxE-SS, respectively. AX1 represented yield potential; AX2 was related to soil conditions, aerobic status and possibly VPD; and AX3 to change in phenology (days to flowering) with stress. The four environment groups were considered as broadly representative of contrasting rice production environments, including lowland-type, upland-wet season, and upland-aerobic environments that experienced vegetative- or anthesis-stage drought stress. Genotype groups differed in adaptation to these diverse environments. For genotype groups G1 to G6, G3 (VM150) had stable yields across environments; G1 (VM134) had the greatest grain yield in lowland-type environments (E2); G5 (VM135) in wet season environments (E3); G6 (VM168) in anthesis-stage drought (E4); G2 (Vandana and VM26) in vegetative- and anthesis-stage drought (E1 and E4); and G4 had average yields across environments. Implications for breeding of rice adapted to contrasting hydrological environments are discussed, with the caution that adaptation to more than one environment type is desirable, because, as is demonstrated in this paper, an untimely climatic event can transform one environment type into another. Our results suggest that selection in one environment type may not give benefit in other environment types, so testing in more than one environment type is essential.

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Abstract

Genotype by environment (G × E) interactions were investigated in Vandana and a subset of 13 BC2 and BC3 lines of an improved indica upland rice cultivar, Vandana, backcrossed with a drought-tolerant traditional japonica cultivar, Moroberekan, which has a thick and extensive root system, in response to eight hydrological field environments conducted at Los Baños, in the Philippines, between 2001 to 2003. The G × E interaction accounted for 13% of the total sum of squares with environment and genotype responsible for 84 and 3%, respectively. Cluster analysis identified four environment and six genotype groups, which accounted for 70% of the G × E sums of squares. Of this, AX1, AX2 and AX3 accounted for 27, 22 and 21% of the G x E-SS, respectively. AX1 represented yield potential; AX2 was related to soil conditions, aerobic status and possibly VPD; and AX3 to change in
phenology (days to flowering) with stress. The four environment groups were considered as broadly representative of contrasting rice production environments, including lowland-type, upland-wet season and upland-aerobic environments that experienced vegetative- or anthesis-stage drought stress. Genotype groups differed in adaptation to these diverse environments. For genotype groups G1 to G6, G3 (VM150) had stable yields across environments; G1 (VM134) had the greatest grain yield in lowland-type environments (E2); G5 (VM135) in wet season environments (E3); G6 (VM168) in anthesis-stage drought (E4); G2 (Vandana and VM26) in vegetative- and anthesis-stage drought (E1 and E4); and G4 had average yields across environments. Implications for breeding of rice adapted to contrasting hydrological environments are discussed, with the caution that adaptation to more than one environment type is desirable, because, as is demonstrated in this paper, an untimely climatic event can transform one environment type into another. Our results suggest that selection in one environment type may not give benefit in other environment types, so testing in more than one environment type is essential.

Keywords: Drought response; Upland rice; Roots; Grain yield; Yield components

1. Introduction

Rice is grown in a wide range of environments and is one of the most important food crops world-wide, with 150 million ha of total rice area sown annually (Maclean et al., 2002). Lowland or paddy rice is grown in flooded conditions, whereas upland rice is produced in tropical and sub-tropical rainfed environments in aerobic soils with little or no impounding of water, and is prone to drought when rainfall or soil water reserves are inadequate to meet plant requirements. Around 13 million ha of upland rice is grown in Asia, Latin America and West Africa, and regions that have traditionally grown lowland rice are becoming water-limited due to increased water scarcity (Rijsberman, 2006). The characteristics of drought
events vary across regions. In Eastern India, for example, the short growing season and low and variable rainfall both contribute to terminal drought stress; in West Africa, the wet season is bimodal with drought experienced in July to August; in central Brazil, drought is typical for 5 to 20 d during February and is intensified by the poor water-holding capacity of the soil, an Oxisol (De Datta and Vergara, 1975). The severity of vegetative-stage drought stress will depend on the plant’s ability to avoid stress, for example, through a deeper or more extensive root system, and the ability to recover upon rewatering (O'Toole and Chang, 1979; Yoshida and Hasegawa, 1982). Drought at anthesis can delay or prevent flowering, or result in pollen or spikelet sterility (Saini and Westgate, 2000). A primary target of rainfed rice breeding programs is to develop cultivars with stable grain yield under drought.

Direct selection for yield under drought integrates whole-plant response to water stress, but is complicated by the potentially large interaction of yield with environment (e.g. (Fukai and Cooper, 1995; Wade et al., 1999a; Lafitte and Courtois, 2002). One breeding approach has targeted the development of high-yielding, drought tolerant cultivars by combining selection for high yield potential under favourable aerobic environments in the wet season, with screening for yield under moderate stress during anthesis (Atlin et al., 2006). High yield was associated with the maintenance of high biomass production, spikelet fertility and harvest index under moderate anthesis-stage drought stress (Bouman et al., 2005; Atlin et al., 2006). In contrast, (Lafitte et al., 2006) selected for drought tolerance in a wide range of backcross lines derived from high-yielding indica cultivars and japonica breeding lines in upland, lowland-irrigated and lowland-stress environments. Superior lines possessed various traits, such as continued leaf area development, root growth into moist soil and continued photosynthesis, which conferred adaptation to the contrasting stress environments. Alternatively, research efforts have concentrated on targeting specific traits that could contribute to drought response in the appropriate environment (e.g. (O'Toole and Chang, 1979; Fukai and Cooper, 1995; Lafitte, 1999). Some traits, such as early maturation or a
deeper and thicker root system, may allow the crop to avoid drought (Passioura, 1982; Ekanayake et al., 1985). A more extensive root system enables the crop to extract water located in the deeper soil layers to maintain plant water status and this can contribute to higher yields under drought stress (Mambani and Lal, 1983a). Other traits, such as osmotic adjustment, enable plants to tolerate drought. *Japonica* cultivars typically have poor dehydration tolerance or low osmotic adjustment compared with lowland (*indica*) rice cultivars (Lilley and Ludlow, 1996). While some traits have been shown to confer drought tolerance for a given type of stress, breeding for high yield potential in rice for drought–prone environments remains elusive, because of the complexity in the timing and duration of drought stress in lowland and upland conditions across seasons.

The objective of this study was to use a G × E approach to determine the basis of adaptive response for grain yield in *indica* upland Vandana × Moroberekan backcross lines to diverse environments. This study is unique in that (i) the environments represented a wide range of hydrological states, and included upland wet-season, irrigated and drought-stressed dry season, and flooded lowlands; and (ii) the genotypes evaluated were closely-related BC2 and BC3 lines selected from a larger plant population on the basis of superior grain yield under mild anthesis-stage drought stress, yet varied in yield response to a range of environments. The G × E interactions were thus used to interpret the basis of adaptation of genotype groups to the different environments and, in doing so, provide insight into the selection strategies required for identifying superior germplasm adapted to one or more target environments. At issue is the unpredictable nature of the growing season, how an environment can assume the characteristics of another, depending on the conditions encountered, and what strategies can be used to address this by developing germplasm adapted to more than one type of environment.
2. Materials and methods

2.1 Plant material

The fourteen genotypes comprised thirteen Vandana × Moroberekan BC2 and BC3 lines and the recurrent parent, Vandana. The lines were extracted from a broader Vandana × Moroberekan mapping population of 151 lines on the basis of superior grain yield under mild anthesis-stage drought stress in the 2001 dry season at Los Baños (Lafitte and Courtois, unpublished data). The 13 backcross lines had a predominately Vandana background with only a small (14%, on average) introgression of Moroberekan (Lafitte and Courtois, unpublished data). Vandana is an improved upland indica rice cultivar that was released in India in 1992 (Sinha et al., 1993). The target region for this cultivar is the short-season plateau upland of Eastern India. Vandana is semi-tall (115-130 cm), has good plant vigour, and growth duration of 90-95 d, but is prone to lodging under high moisture and fertility levels. Moroberekan is a traditional japonica cultivar from Guinea with a deep and thick root system and vegetative-stage drought tolerance (Champoux et al., 1995; Ray et al., 1996; Lafitte et al., 2001), late maturity (Lafitte and Courtois, 2002), and poor dehydration tolerance (Lilley and Ludlow, 1996).

2.2 Field

The Vandana × Moroberekan BC2 and BC3 lines and the recurrent parent, Vandana, were evaluated in eight field environments in Los Baños (14°11’N 121°15’E, 21 m above sea level), Philippines, from 2001 to 2003. Trials were conducted in both dry and wet seasons and environments included predominately upland aerobic (well-watered and drought-stressed) conditions and one lowland anaerobic site with ponded water (Table 1). Site selection was consistent with the known upland adaptation of the Vandana and Moroberekan parental lines, with the one lowland site established to assess adaptation in an anaerobic soil environment.
Representation of environments and replicates in the G × E analysis was hence unbalanced, although yield data were extracted from the individual, replicated field trials, as detailed below.

Soil type was an Andaqueptic Haploquol with a pH of 6.5. Dry season trials were sown in January and wet season trials in June. Plot sizes ranged from 1 m x 3 rows (0.75 m) to 3 m x 8 rows (2 m) at a seeding rate of 60 kg ha\(^{-1}\) at upland sites and three transplants per hill at the flooded lowland site. Designs were RCBD, split-plot, augmented or \(\alpha\)-lattice with 2 to 4 replications (Table 1). Aerobic sites were sprinkler irrigated for germination and then drip- or basin-irrigated as required to maintain soil moisture tension below 20 kPa. Basal fertilizer was applied at a rate of 40 kg ha\(^{-1}\) N:P:K and plots were top-dressed with 60 kg N ha\(^{-1}\) (80 kg N ha\(^{-1}\) for lowland environments) split equally between early vegetative growth and at booting. Pests were controlled chemically as required.

For vegetative-stage stress at 03UDNvs, drought was imposed by withholding irrigation once the majority of plants reached the 5-leaf growth stage at 38 DAS. Irrigation was resumed after 30 d. For anthesis-stage stress (01UDN and 02UDN), terminal drought was imposed by turning off drip irrigation to individual plots when plants reached flag leaf exertion. Leaf water potential was measured in the 02UDNas field trial 27 d after stress was imposed, using a Scholander type pressure chamber (Soil Moisture Equipment Corporation, Santa Barbara, California, USA). Soil moisture content was measured at the end of drought stress at this site. Data for soil moisture content and leaf water potential were unavailable for the 01UDNam and 03UDNvs sites. Date of anthesis, plant height, yield and yield components were measured in all environments, except 03UDNvs, where only data for grain yield were available.

Yield data for 14 genotypes (13 Vandana × Moroberekan BC2 and BC3 lines and the recurrent parent, Vandana) and 8 environments were extracted from appropriate single-site analyses for each site. G × E interactions were analysed using the pattern analysis tool in
IRRISTAT (IRRI, 2000). Data for row and column means were location-standardised for analysis. The transformed data were clustered using an agglomerative hierarchical algorithm based on minimising incremental sum of squares (Table 3). Scores for both genotypes and environments from the two-component interaction principal components model were computed for AX1, AX2 and AX3 and plotted as biplots (Figs. 3 and 4). Yield components and biomass partitioning during vegetative growth were grouped according to clusters identified by pattern analysis (groups) and assessed for effects of environment, group, genotype, environment × group and environment × genotype interactions using the GLM procedure in SAS (SAS Institute Inc., 1990).

2.3 Glasshouse

Three Vandana × Moroberekan BC2 (VM135, VM168) and BC3 (VM26) lines, and the recurrent parent, Vandana, were sown in a glasshouse trial to assess anthesis-stage drought effects on biomass partitioning to roots and root growth rate. Four pre-germinated seeds were sown into pots (0.8 tall × 0.25 m diameter) lined with a plastic sleeve and filled with potting mix (soil: coir dust: sand) with 4 replicates in a RCBD in the glasshouse. Pots were watered daily until 65 DAS. One third of the pots were harvested at the start of drought stress; remaining pots were divided into two treatments: well-watered or receiving no further irrigation. Pot water-use were measured by weighing daily after stress imposition until 87 DAS. At harvest, roots were washed, dried and weighed. Data were analysed for effects of treatment, genotype and treatment × genotype interactions using the GLM procedure in SAS (SAS Institute Inc., 1990).
3. Results

3.1 Characterisation of environments

The IRRI Experiment Station in Los Baños is located in the tropics and has a distinct dry (January to May) and wet season (June to November) (Table 2). The hottest months occur in the dry season from March to April when there are few rainfall events, high radiation levels and high vapour pressure deficit (VPD).

Two aerobic, dry-season environments, 01UDI and 02UDI, were irrigated, and two were not, 01UDNam and 02UDNas. The 01UDNam environment experienced mild anthesis-stage drought stress, on account of large rainfall events in February and May. In contrast, the 02UDNas environment experienced severe anthesis-stage drought stress, with less than the average rainfall occurring from planting through to April. During the 02UDNas, the average midday leaf water potential of selected lines at 27 d after stress was imposed reached -2.2 MPa in the well-watered treatment, and –3.0 MPa under stress. Soil moisture content at a depth of 0 – 30 cm and 30 – 45 cm was reduced by 30% and 18%, respectively, compared with well-watered plots at the end of the stress period. The aerobic 03UDNvs environment experienced severe vegetative-stage drought stress as the site received only 10 mm of rainfall during the 30 d stress period.

The single lowland environment, 01UDIp, had ponded water and the soil was anaerobic. The remaining two environments, 01UWN and 02UWN, were grown under upland rainfed conditions in the 2001 and 2002 wet seasons. The wet season received close to three times the rainfall of the dry season; VPD and radiation were 12 and 15% lower, respectively, in the wet season. Both wet seasons had a rain-free period that increased soil moisture tension to 60 kPa (Table 2).

3.2 Analysis of variance and pattern analysis of grain yield
Mean grain yields were computed for each environment using the appropriate analysis for each trial. These means were extracted for the eight environments and fourteen genotypes. For grain yield, genotype main-effects accounted for only 3% of the total sum of squares, with environment 84%, and the G × E interactions 13% (Table 3). Hence, the sum of squares for G × E was 4 times that for G. Cluster analysis on the location-standardised residuals was used to identify four environment groups (Fig. 1) and six genotype groups (Fig. 2). This combination preserved 70% of the G x E-SS among groups. The ordination analysis of the location-standardised residuals indicated that interaction principal component axes AX1, AX2 and AX3 accounted for 27, 22 and 21% of the G x E-SS, respectively (Table 3). The relationships between AX1 and AX2, and between AX1 and AX3, are shown in Figs. 3 and 4, and are described in the following sections.

3.3 Main effects of environment on grain yield and yield components

Four environment groups were identified by cluster analysis in Fig. 1. Environment E1, which included the only singleton, 03UDNvs (referred to, for simplicity, as the ‘vegetative-stage drought group’, E1), experienced severe vegetative-stage drought stress and yielded only 58 g m⁻² compared with the equal largest mean grain yield in groups E2 and E3 (Table 5). Environment E2, (referred to as the ‘lowland-type group’, E2), included the only flooded, anaerobic site, 02LDIp, and 01UDI. The 01UDI site was intended to represent an irrigated, upland (aerobic) environment in the dry season. However, 5.5 and 1.5 times the average rainfall in February (tillering) and May (grain filling) 2001, respectively, (Table 2), may have resulted in brief periods of waterlogging consistent with soil conditions commonly encountered in irrigated-lowland and rainfed-lowland conditions. Environment E3, included the two wet-season sites, 01UWN and 02UWN (‘wet-season group’, E3). Environment E4 included aerobic sites 01UDNam, 02UDNas and 02UDI (‘anthesis-stage drought group’, E4), which all experienced varying degrees of water stress at anthesis. Similar to 01UDI, the
intended environment of the 02UDI site was an irrigated, upland (aerobic) environment in the dry season. However, high evaporative demand in this season may have resulted in mild stress when the canopy was large, despite drip irrigation, and hence, grouping this site with the two sites experiencing anthesis-stage drought stress.

The four environment groups (Fig. 1) are clearly separated by the three principal component axes in Figs. 3 and 4. For AX1, the vegetative-stage drought group (E1) was strongly negative, and the wet-season group (E3) was strongly positive, while the lowland-type group (E2) was neutral (Fig. 3 or 4). The anthesis-stage drought group (E4) was neutral to mildly and strongly positive for AX1. For AX2, the anthesis-stage drought group (E4) was strongly positive and the lowland-type group (E2) strongly negative, while the vegetative-stage drought group (E1) and wet-season group (E3) were neutral to mildly negative, respectively (Fig. 3). For AX3, anthesis-stage drought stress (E4) and lowland-type (E2) groups were strongly to mildly positive, the vegetative-stage drought stress group (E1) was neutral and the wet-season group (E3) neutral to slightly negative (Fig. 4).

Main effects, but not the interaction, were significant for environment for anthesis date, plant height and yield components, including above-ground DM, thousand grain weight, number of panicles, grain panicle$^{-1}$ and grains m$^{-2}$ (Table 4). Drought applied in the 03UDNvs experiment at 39 DAS greatly increased the duration of tillering and delayed flowering. Consequently, above-ground DM was much less and there was a larger proportion of dead leaves in the 03UDNvs compared with other environments (data not shown). Anthesis date was on average 4 d later in the lowland-type (E2) and wet-season (E3) groups than the anthesis-stage drought group (E4) (Table 4). Transplanting shock in the 02LDIp site would have contributed to this, and in the wet season, the later maturity may have resulted from a comparatively lower temperature compared with the dry season. Anthesis date was negatively correlated with panicles m$^{-2}$ (r = -0.75*) and the proportion of sterile panicles (r = -0.83*)
across environments. A significant negative association was observed between harvest index and anthesis date in the four environments (average $r = -0.63^*$) (data not shown).

Plants were tallest in the wet-season group (E3) and had greater above-ground DM than other environments (Table 4). Later flowering in the flood-irrigated group (E2) (Table 4) was associated with increased total biomass in the 01UDI site, whereas plant height was comparably shorter, in part due to lower plant population in the 02LDIp but also to smaller plant size (data not shown). Lodging was widespread in both wet season experiments, in the lowland, and for some lines when stress was imposed.

Fewer panicles (30% less), but more grain m$^{-2}$, were produced in the lowland-type (E2) and wet-season (E3) groups, than in the anthesis-stage drought group (E4) (Table 4). Environment had a large effect on spikelet fertility, and in the anthesis-stage drought group (E4), reduced the number of grain per panicle and produced smaller grain than wet-season group (E3) (Table 4).

3.4 Main effects of genotype on grain yield and yield components

Six genotype groups were identified by cluster analysis in Fig. 2. Three of the six genotype groups, VM134 (G1), VM150 (G3) and VM135 (G5), were singletons. VM26 and Vandana together formed genotype group ‘Vandana’ (G2). The remaining genotypes were grouped in ‘VM38’ (G4, including VM29, VM38, VM96, VM103, VM128 and VM129) and ‘VM168’ (G6, including VM17, VM73 and VM168).

These six genotype groups were clearly separated by the three principal component axes shown in Figs. 3 and 4. For AX1, VM134 (G1) and VM150 (G3) were strongly negative and VM135 (G5) strongly positive, while Vandana group (G2) was mildly negative and VM168 group (G6) mildly positive (Fig. 3). For AX2, VM134 (G1) was strongly negative, VM38 group (G4) and VM135 (G5) were slightly negative, while Vandana group (G2), VM150 (G3) and VM168 group (G6) were all slightly positive (Fig. 3). For AX3, Vandana
group (G2), VM134 (G1) and VM135 (G5) were all positive, while VM150 (G3), VM38 group (G4) and VM168 group (G6) were all negative. Genotypes VM134 (G1) and VM135 (G5) had the largest mean grain yield across genotype groups (Table 5), although days to anthesis in VM135 (G5) was 13 d later than Vandana in the lowland and wet season sites (data not shown). Genotype VM150 (G3) flowered later and was tallest, yet had the lowest mean grain yield of 184 g/m² (Table 5), as grain were small in size and few panicles tended to be produced per plant (Table 4).

VM26 and Vandana were tallest and interacted similarly with environment in terms of yield, yet AX3 separated VM26 (strongly positive) from G1-VM134, G5-VM135 and G2-Vandana (intermediate) and the rest (neutral-negative) (Fig. 4). With the exception of the 02UWN, anthesis date of VM26 was 7 to 15 d later than Vandana across environments, leading to an additional 4 to 18 cm in height and 23 to 43% more biomass than Vandana (data not shown). Tall plant height of VM26 was expressed only in irrigated (01UDI) or mild anthesis drought-stress conditions in the 01UDNam and 02UDI environments, and not in flooded lowlands 02UDIp, the wet season E3 or under severe anthesis-stage drought stress in the 02UDNas experiments (data not shown).

3.5. Grain yield and yield components of six genotype groups in four environment groups

Genotype VM150 (G3) had the greatest biomass production but the lowest grain yield in all conditions except in the vegetative-stage drought group (E1), and hence consistently low harvest index (HI) (Table 5). Vandana group (G2) and VM168 group (G6) maintained spikelet fertility and grain yield under drought stress in the anthesis-stage drought group (E4) to produce a higher HI than remaining genotype groups (Table 5). In contrast, genotype VM134 (G1) and VM135 (G5) had larger grain yield and HI in the lowland-type (E2) and wet-season (E3) sites, when water was readily available (Table 5). Relatively poor spikelet
fertility of VM38 group (G4) was mainly attributed to an 18% loss of fertility in the line VM129 across environments (data not shown).

3.6 Root biomass and growth rate during anthesis-stage drought stress in pots

Average total root DM per plant at the start of drought stress across genotypes was 2.6 g. Total root DM more than doubled from 65 to 86 DAS in well-watered, but root growth rate was 46% slower under drought stress and hence plants had less total root DM compared to well-watered plants (Table 6). Backcross lines VM135 and VM168 produced more total root DM at 65 DAS than Vandana or VM26 (Table 6). Vandana and VM135 had the fastest rate of root growth from 65 to 87 DAS and the largest total root DM under well-watered conditions, but rate of growth fell the greatest in these entries under drought stress (Table 6). In contrast, root growth rate of VM168 was 25% slower under well-watered conditions than Vandana, but was relatively stable under drought stress (Table 6). Daily pot water-use was the same for all entries 7 days after the start of drought stress (data not shown). Cumulative water use was greatest for VM26 (4.30 kg) and lowest for Vandana (3.88 kg).

4. Discussion

Consistent with the diverse hydrological environments and genetic similarity of the Vandana x Moroberekan backcross lines evaluated in this study, main effects of environment on grain yield were large and dominated the total sum of squares. However, the G × E interaction accounted for 13% of the total sum of squares and was four times greater than the main effect of genotype. Large G × E sum of squares relative to G are consistent with other studies, albeit of genetically-diverse rice cultivars, conducted in both upland (Lafitte and Courtois, 2002; Atlin et al., 2006) and rainfed-lowland environments (Cooper et al., 1999; Wade et al., 1999b). Three vectors accounted for 70% of GxE, suggesting a high repeatable component, which was consistent with other studies in rice (Wade et al., 1999b). The
implications of these G × E interactions for grain yield of these upland backcross lines for
genotypic evaluation of rice cultivars within and across environments are discussed below.

4.1 Environment groupings

The eight environments were grouped by cluster and principal component analysis
into four distinct groups that can be defined according to their hydrology. The four
environment groups were positioned at opposite extremes of the principal component axes
AX1 and AX2, similar to the four points of a compass. The vegetative-stage drought (E1) and
wet-season (E3) groups were separated by AX1, and the lowland-type (E2) and anthesis-stage
drought (E4) groups by AX2. Genotypes that had large grain yields within the anthesis-stage
drought group (E4) were further separated by AX3. These four environment groups can be
shown to be representative of several major ecosystems, including irrigated-lowland, rainfed-
upland and upland-aerobic environments that experienced vegetative- or anthesis-stage
drought stress. The adaptation of genotypes to these diverse hydrological environments is
discussed in section 4.2.

Grain yields in favourable environments, such as the wet-season group (E3, positive
on AX1), were comparable with those reported in the literature for upland (Lafitte et al.,
2002; Atlin et al., 2006) and aerobic (Bouman et al., 2006) environments. The wet-season
group (E3) not only received reliable to high rainfall, but had a low vapour pressure deficit
that was conducive to high biomass production and hence grain yield. We consider the wet-
season group (E3) to thus be representative of rainfed-upland ecosystems during the wet
season. In contrast, the lowland-type group (E2, negative on AX2) had either ponded water or
experienced greater than average rainfall in February and May that could have resulted in
brief periods of waterlogging. These anaerobic soil conditions, or anaerobic-aerobic soil
transitions, are considered to be broadly representative of irrigated-lowland or rainfed-
lowland ecosystems. Grain yield of these upland rice cultivars and breeding lines in the
01UDIp environment was much less, as could be expected, than those of adapted lowland or rainfed-lowland rice cultivars (e.g. (Wade et al., 1999b; Bouman et al., 2006). Upland rice typically tillers less and roots have fewer aerenchyma than adapted lowland cultivars when grown under flooded, anaerobic conditions (Kondo et al., 2000). Furthermore, the change from aerobic to anaerobic or from aerobic to anaerobic soil status associated with transitory waterlogging, as occurs in rainfed-lowland environments, is reported to have a significant negative impact on crop growth and grain yield of rice (Jearakongman et al. 1995; Wade et al., 1998; Fukai et al., 1999; Wade et al., 1999b).

Grain yield in the vegetative- (E1) and anthesis-stage drought (E4) groups were 21 and 75% relative to the highest-yielding wet-season sites (E3), respectively. Both groups were representative of upland, aerobic ecosystems and differed in the timing and severity of drought stress. The impact of timing and severity of water stress during crop development of rice on yield and components of yield are well established. Early stress, occurring during vegetative growth, can interrupt floret initiation, while drought during flowering causes spikelet sterility, and terminal drought effects grain filling (Ekanayake et al., 1989; Lilley and Fukai, 1994c; Kamoshita et al., 2001; Lafitte, 2002; Pantuwan et al., 2002; Kamoshita et al., 2004).

4.2 Adaptation of genotype groups to diverse hydrological environments

The G × E approach employed in this analysis permits multiple comparisons of adaptation of genetically-similar backcross lines to diverse hydrological environments. These contrasts are typically restricted in the literature to comparisons of adaptation of genetically-diverse cultivars within one or, occasionally, two of the major ecosystems. More is possible here, because seasonal conditions encountered in this study increased the diversity of environments sampled. This, however, reflects reality in unpredictable seasons, allowing consideration of the implications for selection in section 4.3.
It was particularly interesting that the G × E analysis identified six genotype groups, despite the backcross lines being selected on the basis of grain yield under mild anthesis-stage drought stress and sharing a predominately Vandana background of, on average, 84%. This highlights the importance of relatively-small genetic differences to plant adaptation in diverse environments. Four of the six genotype groups VM134 (G1), VM150 (G3), VM135 (G5) and VM168 group (G6) clearly differed in their interaction with the principal component axes and hence in adaptation to environment. These four genotype groups were characterised by improved yield in contrasting environments; VM134 (G1) to the anaerobic soil conditions of irrigated-or rainfed-lowlands, VM135 (G5) to rainfed-upland ecosystems in the wet season, and VM150 (G3) and VM168 group (G6) to upland vegetative - and anthesis-stage drought stress, respectively. Accordingly, late-maturing VM150 (G3), the most tolerant of vegetative-stage drought stress, produced more fertile spikelets and the greatest grain yield under these conditions. A contributing factor to anthesis-stage drought tolerance was stability of root growth rate and total root dry matter compared with well-watered conditions, as shown by VM168 (G6).

In genotype groups VM134 (G1) and VM135 (G5), which were adapted to irrigated-lowland and rainfed-upland environments, respectively, a longer duration and tall plant height combined to maximise biomass production, grains per panicle and hence grain yield. Days to anthesis in VM135 (G5) were 13 d later than Vandana in these environments, a trait presumably derived from the late-flowering Moroberekan. Greater grain yield of VM135 (G5) in wetter environments was through a combination of factors which, while not significant individually, together resulted in a high yield potential when ample water was available. The lines that performed well in these environments also tended to have greater root mass in well-watered conditions, but root growth was greatly reduced by drought. Consistent with previous findings, plants in VM134 (G1) and VM135 (G5) under anthesis-stage drought stress were short, with a low harvest index and a larger proportion of sterile florets (Lilley and Fukai,
1994c; Lafitte and Courtois, 2002). These data indicate that it is possible to combine the
greater root mass of Moroberekan with the short growth duration of Vandana for higher yield
in more favourable conditions, as hypothesised by (Champoux et al., 1995), but when stress is
severe this strategy may not be effective in sustaining grain yield. Under severe stress,
strategies such as root signals and stomatal closure have been demonstrated to meter the loss
of water as water deficit progresses (Siopongco et al., 2008).

The Vandana group (G2) was adapted to upland vegetative- and anthesis-stage drought
environments. However, adaptation to severe drought stress was not as strong as for VM150
(G3), which had the largest grain yield at this site. The third axis, AX3, contributed to a
significant proportion of the total G × E sum of squares and was a source of differentiation
between the two Vandana (G2) genotypes, most likely on the basis of crop duration. The
recurrent parent, Vandana, is a tall cultivar with early maturity, low biomass, and a tendency
to lodge in favourable conditions (Kondo et al., 2003). VM26 had delayed flowering, a
smaller reduction in root growth rate and dry matter, and a slightly higher yield than Vandana
under anthesis-stage drought stress. Consequently it appears that VM26 possesses adaptive
trait(s) for tolerance to anthesis-stage drought stress, while Vandana escapes terminal drought
by early flowering. While greater root biomass may provide an advantage in well-watered
conditions in upland rice, as suggested by our results for large grain yield of VM135 in the
wet seasons, under drought stress this trait may result in rapid depletion of soil water,
reducing crop growth and yield. These traits in VM26 were presumably derived from the
donor, Moroberekan, which is tall and late maturing cultivar with high biomass, and has a
large and thick root system (Champoux et al., 1995; Ray et al., 1996; Lafitte et al., 2001).
These observation are consistent with (Lafitte and Courtois, 2002) and (Atlin et al., 2006),
who reported that early flowering resulted in improved grain yield and spikelet fertility in a
wide range of upland rice cultivars grown in environments with managed and rainfed
anthesis-stage drought stress, respectively.
In summary, it appeared that AX1 represented yield potential (low on left, high on right), which relates secondarily to vegetative stress and restricted DM production on the left, and possible late terminal stress and lodging on the right. AX2 related to soil conditions and aerobic status, with anaerobic periods to the bottom and aerobic to the top. There was also a suggestion of low VPD at the bottom to high VPD at the top. AX3 related to change in phenology (days to flowering) with stress, with little change at the bottom, and a large change at the top. There was a second related consideration of change in plant height or above-ground DM under stress. Environment groups E1 to E4 represented vegetative-stage drought stress, lowland-type, wet season, and anthesis-stage drought stress, respectively. For genotype groups G1 to G6, G3 (VM150) had stable yields across environments; G1 (VM134) had the greatest grain yield in lowland-type environments (E2); G5 (VM135) in wet season environments (E3); G6 (VM168 group) in anthesis-stage drought (E4); G2 (Vandana and VM26) in vegetative- and anthesis-stage drought (E1 and E4); and G4 (VM38 group) had average yields across environments.

4.3 Implications for breeding for plant adaptive response to diverse hydrological environments

The genotype x environment interactions identified within the genetically-similar Vandana x Moroberekan backcross lines have implications for breeding for diverse hydrological environments. Breeders typically select for traits in one environment, or less frequently, in a two-way combination of lowland, upland dry- or wet-season environments (Atlin et al., 2006; Lafitte et al., 2006). However, a target environment may vary over a series of seasons, such as occurred here. The G × E analysis clearly delineated four environment and six genotype groups, even though the backcross lines had a predominately Vandana background. Consequently, success of a line in one stress environment does not seem likely to confer success in others based on our evidence. While breeders target the dominant traits
expected with highest probability for that environment, it would be advantageous if there was a capacity to cope with other conditions, so the cultivar would not fail in the event, for example, of an untimely rainfall transforming aerobic rice to rainfed lowland. This may require testing in more than one environment type, in order to achieve yield stability. Lines typical of particular genotype groups can also be used as reference lines for selection nurseries, to help in assessing lines for target environments (Fox and Rosielle, 1982; Wade et al., 1996). Furthermore, the genotypes examined here will be suitable candidates for further studies to understand the mechanisms that allow them to have preferential adaptation to contrasting hydrological environments. Contrary to the assertion of Venuprasad et al. (2008), progress in breeding for yield in one environment may not give benefit in other rice ecosystems, based on the evidence shown here. Essentially, there is a continued need to evaluate breeding materials in a range of conditions; it is not sufficient to assess germplasm intended for multiple ecosystems in a single environment type.

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contrasting water-deficit regimes I. Root distribution, water use and plant water status.

Field Crops Res. 76, 11-24.


**Figure captions**

Fig. 1. Environment groupings applied to standardised yield data for 13 Vandana x Moroberekan BC3 and BC4 backcross lines, and the recurrent parent, Vandana (V). The dendrogram shows fusion levels at which the groups join. The fusion level is proportional to the increase in pooled within group SS at each fusion. The vertical dashed line represents the truncation of 8 environments into 4 groups using Ward’s agglomerative clustering algorithm. Refer to Table 1 for environment abbreviations.

Fig. 2. Genotype groupings applied to standardised yield data for 13 Vandana x Moroberekan BC3 and BC4 backcross lines, and the recurrent parent, Vandana (V) over 8 environments. The dendrogram shows fusion levels at which the groups join. The fusion level is proportional to the increase in pooled within group SS at each fusion. The vertical dashed line represents the truncation of 14 genotypes into 6 groups using Ward’s agglomerative clustering algorithm.

Fig. 3. Principal component analysis (location standardised) for the environment × genotype interaction for AX1 and AX2 for grain yield for 8 environments, 13 Vandana x Moroberekan BC3 and BC4 backcross lines, and the recurrent parent, Vandana (V). Refer to Table 1 for environment abbreviations. The G × E interaction for AX1 and AX2 accounted for 48.8% of the sums of squares.
Fig. 4. Principal component analysis (location standardised) for the environment × genotype interaction for AX1 and AX3 for grain yield for 8 environments, 13 Vandana x Moroberekan BC3 and BC4 backcross lines, and the recurrent parent, Vandana (V). Refer to Table 1 for environment abbreviations. The G × E interaction for AX2 and AX3 accounted for 43% of the sums of squares.
Table 1

Environment, treatment and sowing date of the eight field experiments undertaken in Los Baños (Philippines) for 2001-03.

<table>
<thead>
<tr>
<th>Code</th>
<th>Year</th>
<th>Environment</th>
<th>Season</th>
<th>Irrigation</th>
<th>Stage and severity of stress</th>
<th>Design</th>
<th>Reps</th>
<th>Plot size</th>
<th>Plant Spacing (m)</th>
<th>Sowing date</th>
</tr>
</thead>
<tbody>
<tr>
<td>01UDNam</td>
<td>2001</td>
<td>Upland</td>
<td>Dry</td>
<td>Drip</td>
<td>Anthesis, mild</td>
<td>Split-plot</td>
<td>2</td>
<td>3m x 4 rows</td>
<td>0.10</td>
<td>29 Jan</td>
</tr>
<tr>
<td>01UDI</td>
<td>2001</td>
<td>Upland</td>
<td>Dry</td>
<td>Drip</td>
<td></td>
<td>Split-plot</td>
<td>2</td>
<td>3m x 4 rows</td>
<td>0.10</td>
<td>29 Jan</td>
</tr>
<tr>
<td>01UWN</td>
<td>2001</td>
<td>Upland</td>
<td>Wet</td>
<td>Rainfed</td>
<td></td>
<td>RCBD</td>
<td>3</td>
<td>3m x 4 rows</td>
<td>0.10</td>
<td>21 Jun</td>
</tr>
<tr>
<td>02LDIp</td>
<td>2002</td>
<td>Lowland</td>
<td>Dry</td>
<td>Ponded</td>
<td></td>
<td>RCBD</td>
<td>2</td>
<td>3m x 4 rows</td>
<td>0.25</td>
<td>24 Jan</td>
</tr>
<tr>
<td>02UDI</td>
<td>2002</td>
<td>Upland</td>
<td>Dry</td>
<td>Drip</td>
<td></td>
<td>Split-plot</td>
<td>2</td>
<td>3m x 4 rows</td>
<td>0.10</td>
<td>28 Jan</td>
</tr>
<tr>
<td>02UDNas</td>
<td>2002</td>
<td>Upland</td>
<td>Dry</td>
<td>Drip</td>
<td>Anthesis, severe</td>
<td>Split-plot</td>
<td>2</td>
<td>3m x 4 rows</td>
<td>0.10</td>
<td>28 Jan</td>
</tr>
<tr>
<td>02UWN</td>
<td>2002</td>
<td>Upland</td>
<td>Wet</td>
<td>Rainfed</td>
<td></td>
<td>α-lattice</td>
<td>3</td>
<td>3m x 8 rows</td>
<td>0.10</td>
<td>20 Jun</td>
</tr>
<tr>
<td>03UDNvs</td>
<td>2003</td>
<td>Upland</td>
<td>Dry</td>
<td>Basin</td>
<td>Vegetative, severe</td>
<td>augmented</td>
<td>4</td>
<td>1m x 3 rows</td>
<td>0.10</td>
<td>26 Jan</td>
</tr>
</tbody>
</table>

1 Abbreviations: 01, 2001; 02, 2002; 03, 2003; U, upland; L, lowland; D, dry season; W, wet season; I, irrigated; N, not irrigated; v, vegetative-stage drought stress; a, anthesis-stage drought stress; m, mild; s, severe; p, ponded water;

2 Crop establishment used sprinkler irrigation

3 0.25 m between rows, all environments
Table 2
Long term average monthly weather statistics for IRRI wetland sites from 1979 to 2003, including minimum and maximum air temperature, solar radiation, vapour-pressure deficit (VPD) and rainfall. Monthly rainfall is shown for years 2001 to 2003.

<table>
<thead>
<tr>
<th>Year</th>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>Mean</th>
<th>Jun</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
<th>Oct</th>
<th>Nov</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature (°C)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum</td>
<td>29.5</td>
<td>30.6</td>
<td>32.2</td>
<td>34.0</td>
<td>34.2</td>
<td>32.1</td>
<td>33.0</td>
<td>31.8</td>
<td>31.6</td>
<td>31.7</td>
<td>31.2</td>
<td>30.4</td>
<td>31.6</td>
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<td>21.8</td>
<td>22.4</td>
<td>23.7</td>
<td>24.3</td>
<td>22.8</td>
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<td>23.7</td>
<td>23.7</td>
<td>23.6</td>
<td>23.4</td>
<td>23.7</td>
</tr>
<tr>
<td>Radiation (MJ m⁻²)</td>
<td>14.3</td>
<td>17.2</td>
<td>20.0</td>
<td>21.6</td>
<td>20.0</td>
<td>18.6</td>
<td>17.8</td>
<td>16.4</td>
<td>16.2</td>
<td>16.0</td>
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</tr>
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<td>VPD (kPa)</td>
<td>0.46</td>
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<td>0.83</td>
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<td>0.67</td>
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<td>0.48</td>
<td>0.49</td>
<td>0.49</td>
<td>0.53</td>
</tr>
<tr>
<td>Rainfall (mm)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2001</td>
<td>15</td>
<td>153</td>
<td>51</td>
<td>38</td>
<td>223</td>
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<td>308</td>
<td>200</td>
<td>324</td>
<td>111</td>
<td>177</td>
<td>260</td>
<td>1380</td>
</tr>
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<td>24</td>
<td>8</td>
<td>111</td>
<td>167</td>
<td>79</td>
<td>623</td>
<td>209</td>
<td>205</td>
<td>174</td>
<td>153</td>
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<td>2003</td>
<td>10</td>
<td>4</td>
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<td>10</td>
<td>366</td>
<td>400</td>
<td>245</td>
<td>332</td>
<td>251</td>
<td>245</td>
<td>318</td>
<td>242</td>
<td>1633</td>
</tr>
<tr>
<td>1979-03</td>
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<td>27</td>
<td>42</td>
<td>47</td>
<td>140</td>
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<td>245</td>
<td>332</td>
<td>251</td>
<td>245</td>
<td>318</td>
<td>242</td>
<td>1633</td>
</tr>
</tbody>
</table>

Daily temperatures are averaged over years. Average rainfall is the long-term average 1979-01.
Table 3
Across site ANOVA for 2001 – 2003 G x E interaction studies in diverse rice systems at Los Baños, The Philippines

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>%TSS</th>
<th>% G x E SS</th>
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<tr>
<td>Environment (E)</td>
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<td>136774.82</td>
<td>82.81 ***</td>
<td>84</td>
<td>-</td>
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<tr>
<td>Genotype (G)</td>
<td>13</td>
<td>2688.02</td>
<td>1.63 ns</td>
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<tr>
<td>G x E</td>
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<td>1651.74</td>
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<td>-</td>
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<td>Stability regression</td>
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<td>2251.04</td>
<td>1.45 ns</td>
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<tr>
<td>Regression deviations</td>
<td>78</td>
<td>1551.86</td>
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<td>-</td>
<td>81</td>
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<tr>
<td>AMMI component 1</td>
<td>19</td>
<td>1.45</td>
<td>2.07 *</td>
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<tr>
<td>AMMI component 2</td>
<td>17</td>
<td>1.36</td>
<td>1.94 *</td>
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</tr>
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<td>1.47</td>
<td>2.10 *</td>
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<td>AMMI component 4</td>
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<td>0.96</td>
<td>1.37 ns</td>
<td>-</td>
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<tr>
<td>AMMI residual</td>
<td>76</td>
<td>0.70</td>
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<td>-</td>
<td>18</td>
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</table>
Table 4
Main effect of environment and genotype grouping on yield components of Vandana x Moroberekan BC3 and BC4 lines and the recurrent parent, Vandana. Refer to Figs. 1 and 2 for environment and genotype groups, respectively.

<table>
<thead>
<tr>
<th>Group</th>
<th>Anthesis (DAS)</th>
<th>Plant height (cm)</th>
<th>Above-ground DM (g m⁻²)</th>
<th>Panicles (m⁻²)</th>
<th>Grain Panicle⁻¹</th>
<th>Grain number m⁻²</th>
<th>Grain weight (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>E1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>E2</td>
<td>62</td>
<td>99</td>
<td>838</td>
<td>240</td>
<td>54</td>
<td>12 960</td>
<td>23</td>
</tr>
<tr>
<td>E3</td>
<td>65</td>
<td>121</td>
<td>902</td>
<td>256</td>
<td>48</td>
<td>12 288</td>
<td>22</td>
</tr>
<tr>
<td>E4</td>
<td>59</td>
<td>90</td>
<td>753</td>
<td>348</td>
<td>29</td>
<td>10 092</td>
<td>19</td>
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<tr>
<td>G1</td>
<td>65</td>
<td>96</td>
<td>815</td>
<td>314</td>
<td>42</td>
<td>13 188</td>
<td>21</td>
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<tr>
<td>G2</td>
<td>61</td>
<td>103</td>
<td>882</td>
<td>276</td>
<td>44</td>
<td>12 144</td>
<td>21</td>
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<td>G3</td>
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<td>106</td>
<td>933</td>
<td>268</td>
<td>43</td>
<td>11 524</td>
<td>19</td>
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<tr>
<td>G4</td>
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<td>96</td>
<td>786</td>
<td>277</td>
<td>43</td>
<td>11 911</td>
<td>21</td>
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<tr>
<td>G5</td>
<td>63</td>
<td>99</td>
<td>906</td>
<td>293</td>
<td>47</td>
<td>13 771</td>
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<tr>
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<td>316</td>
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<td>22</td>
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<td>6</td>
<td>ns</td>
<td>ns</td>
<td>7</td>
<td>1 950</td>
<td>1</td>
</tr>
</tbody>
</table>


Table 5
Grain yield, sterile panicles and harvest index of six genotype groups across three environment groups. The overall mean grain yield was 202 (g m$^{-2}$). Data for environment group E1 (03UDNvs) was not available. The l.s.d at $P = 0.05$ for $A = 15$, $AB = 1.0$ and $C = 4$

<table>
<thead>
<tr>
<th>Environment group</th>
<th>Genotype group</th>
<th>Grain yield (g m$^{-2}$)</th>
<th>Sterile panicles (%)</th>
<th>Harvest index</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>G1</td>
<td>G2</td>
<td>G3</td>
<td>G4</td>
</tr>
<tr>
<td>E1</td>
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<td>41</td>
</tr>
<tr>
<td>E2</td>
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<td>259</td>
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<td>270</td>
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<tr>
<td>E3</td>
<td>270</td>
<td>231</td>
<td>230</td>
<td>276</td>
</tr>
<tr>
<td>E4</td>
<td>197</td>
<td>233</td>
<td>192</td>
<td>167</td>
</tr>
<tr>
<td>Mean A</td>
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<td>200</td>
<td>182</td>
<td>189</td>
</tr>
<tr>
<td></td>
<td></td>
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</tr>
<tr>
<td>E1</td>
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<td>E2</td>
<td>7.3</td>
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<tr>
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<td>9.0</td>
<td>14.8</td>
<td>15.2</td>
</tr>
<tr>
<td>Mean B</td>
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<td>Mean C</td>
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Biological partitioning to roots and root growth rate of selected Vandana x Moroberekan BC3 and BC4 lines, and the recurrent parent, Vandana, grown under anthesis-stage drought stress in pots in the glasshouse. Roots were sampled 22 d after the start of drought stress. Abbreviations; WW, well watered; DS, drought stress.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Group</th>
<th>Root DM (g plant⁻¹)</th>
<th>Root growth rate (g plant⁻¹ d⁻¹)</th>
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