Evaluation of upland and lowland rice root morphology for drought tolerance

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Abstract
Drought is a major abiotic constraint to rice production in rainfed and dryland cropping systems. However, root morphological characteristics such as root-to-shoot ratio, root weight distribution, root length density and specific root length have been established as constituting factors for drought tolerance. We compared two upland rice varieties Moroberekan and *Oryza glaberrima* and one lowland rice variety IR64 for drought tolerance under simulated tropical conditions. Irrigation regimes included the well-watered and drought treatment, which had its soil water profile gradually lowered followed by complete withdrawal of water. Upland rice varieties were more drought tolerant based on their root morphological traits and ability to extract water during drought. IR64 modified its root architecture to mitigate the adverse drought effects. This shows that genotypic variation in root system characteristics has significant implications for water and nutrient uptake under resource-constrained environments. Exploiting this genotypic plasticity is vital for breeding resource-use efficient rice varieties.

Keywords: Abiotic stress, root traits; rainfed cropping systems, dryland farming, resource-use efficiency.

Introduction
The world's population is increasing rapidly yet food crop harvests worldwide are threatened by impacts of climate change like drought. By 2050 with 9 billion people to feed there is need to increase crop productivity. We need to produce 40% more rice by 2030 to satisfy this growing demand sustainably (Khush 2005). Yet drought, a major abiotic constraint, is threatening rice production under rainfed ecosystems (Asch et al. 2005). Drought suppresses plant growth and development through reduced nutrient availability and root growth, which reduces uptake rates significantly causing yield losses (Song & Li 2006). However, drought tolerance is exhibited in some rice varieties (Price et al. 2002) through modification of root systems central to the acquisition of water and nutrients. Root characteristics such as root length density, root thickness, rooting depth and distribution have been identified as constituting factors for drought tolerance (Asch et al. 2005). Despite the large body of literature on water deficit and recent advances in molecular biology techniques, drought tolerance mechanisms remain poorly understood especially the root morphological characteristics in comparison with grain quality and disease resistance, which are governed by major genes (Chaves, Maroco & Pereira 2003). Literature shows that indigenous upland rice varieties are more drought tolerant compared to lowland varieties (Asch et al. 2005). However, the contribution of root pattern and morphological characteristics in upland and lowland rice performance under drought conditions is not well documented. A deeper understanding of the physiological basis of these drought tolerance mechanisms, root system structure, function and the variation between varieties is vital for breeders to identify heritable traits to facilitate the breeding of drought tolerant varieties adaptable to arid and semi-arid tropical conditions (Jones 2006). Moreover, information about root morphology and distribution is indispensable for characterisation and modelling of water and nutrient uptake and biomass or crop yield. Efforts to improve existing rice varieties through elucidation of intra-specific drought tolerance mechanisms are important as most climate change scenarios suggest an increase in aridity in many parts of the globe. Here we explore the different root morphological characteristics deployed by upland and lowland rice varieties to mitigate the adverse effects of water deficit on rice productivity.

Materials and methods
The randomised complete block experiment had three varieties, two irrigation regimes and six replicates. Upland rice varieties Moroberekan (tropical upland Japonica variety of Asian origin) and *Oryza glaberrima* (African rice native to sub-Saharan Africa) and lowland rice variety IR64 (semi-dwarf improved variety) were transplanted into 1 m PVC columns with a diameter of 0.12 m filled with a 50:50 soil mixture for rice (high nutrient peat-based compost and high nutrient loam-based compost). The columns fitted with mypex at the bottom were drilled with apertures at 0.1 m, 0.3 m, 0.5 m and 0.7 m from the top to monitor the soil moisture profile using a Theta Probe Soil Moisture Sensor. The well-watered (control) treatment was

maintained at 28% field capacity (FC) whilst the drought treatment instigated at 45 days after planting (DAP) had its soil water profile gradually lowered by reducing the water level in the reservoir by 1 cm over a period of five weeks (35 days) followed by complete withdrawal. Tropical climate conditions were simulated using a Tomtech microclimate controller set to heat the glasshouse at 25^{0}C day and night. The vents automatically opened and closed at 30 ^{0}C during day or night before the temperatures dropped below 27 ^{0}C. Photoperiod was controlled by blackout blinds set to close at 19:00 hours and reopen at 07:00 hours. During the study, soil moisture content was monitored twice a week. At physiological maturity (100 DAP), shoot and root fresh and dry weights were determined. Columns were transversely opened, divided into three layers of 0-30 cm, 30-60 cm and 60-100 cm. Soil from individual layers was extracted and processed for root extraction using a Delta-T-Root Washer. Roots were scanned at 400 dpi resolution and 256 Gray's contrast (TIFF file format) using WinRHIZO STD 1600+ program and analysed using WinRHIZO Regular V.2002C software for total length measurement. Following root scanning and analysis, roots were oven-dried for 48 hours at 85 ^{0}C to determine root dry weights, root-to-shoot ratio, root weight distribution (root dry weight per soil depth), root length density (root length per unit of soil volume) and specific root length (root length per root dry weight). Analysis of Variance was performed using GenStat statistical package to determine treatment effects and their interactions with means deemed significant at a least significant difference of 5%.

Results

Root-to-shoot ratio distribution (R:S ratio)

The R:S ratios were significantly different for both the control and drought treatment ($P = 0.001$) with the control having higher values. Rice variety Moroberekan had the highest R:S ratio (0.203) followed by IR64 (0.156) and *Oryza glaberrima* (0.114), respectively. A similar trend was observed in the drought treatment with Moroberekan having the highest R:S ratio of (0.045) compared with IR64 (0.021) and *Oryza glaberrima* (0.016).

Root dry weight distribution (RWD)

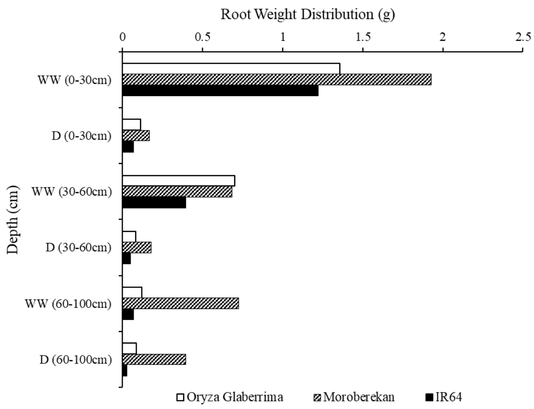
Significant differences in irrigation regimes were observed for RWD at 0-30 cm ($P < 0.001$) and 30-60 cm ($P = 0.023$) depths only with no significant varietal differences. No significant differences in irrigation regimes and varieties were noted at 60-100 cm depth ($P > 0.05$). In the drought treatment, there was a slight reduction in RWD for IR64 and *Oryza glaberrima* at 30-60 cm and 60-100 cm depths. Notably, Moroberekan's RWD increased by over 50% at 60-100 cm depth and *Oryza glaberrima* generally displayed an even distribution of root biomass throughout the soil profile (Figure 1). For the control, there was a reduction in RWD along the soil profile for all varieties except Moroberekan which had relatively similar RWD at 30-60 cm and 60-100 cm depths (Figure 1).

Root length density (RLD)

Despite the significant difference in RLD between the control and drought treatment at 0-30 cm and 30-60 cm ($P < 0.05$), no significant varietal differences and interactions were observed ($P > 0.05$). Differences in varieties were significant at 60-100 cm depth ($P = 0.01$). In the control, Moroberekan had the highest RLD (5), followed by *Oryza glaberrima* (2.5) and IR64 (1.8), respectively (Figure 2). Lowland rice variety IR64 had a higher RLD in the upper soil layers of 0-30 cm and 30-60 cm for the drought treatment. Upland rice varieties particularly Moroberekan had higher root length densities at 60-100 cm depth than IR64 (Figure 2).

Soil moisture content

While soil moisture content varied throughout the experimental period particularly at 0-10 cm ($P < 0.001$), no significant varietal differences and interactions were noted at 0-10 cm and 30-50 cm depths ($P > 0.05$). However, at 10-30 cm depth significant variations in varieties were evident ($P < 0.001$). *Moroberekan* had the highest soil moisture content for the duration of the drought stress, averaging 0.28 m^3m^{-3} followed by *Oryza glaberrima* (0.25 m^3m^{-3}) and IR64 (0.23 m^3m^{-3}), respectively. Interestingly, at 35 days following drought instigation *Oryza glaberrima* and IR64 had the same soil moisture content (0.24 m^3m^{-3}).



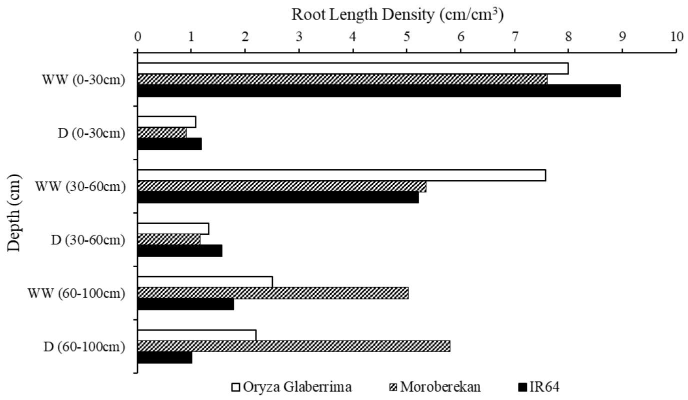


Figure 1. Root weight distribution with depth (SED: 1.4)

Figure 2. Variation of root length density with depth (SED: 0.2)

Specific root length (SRL)

Significant differences in irrigation regimes ($P = 0.011$) and varieties ($P = 0.012$) were evident at 0-30 cm. At 30-60 cm, only significant varietal differences were observed ($P = 0.029$). Specific root lengths were not significantly different for both irrigation regimes and across all varieties at 60-100 cm depth. There was a gradual increase in SRL with depth for both irrigation regimes across all varieties. IR64 had the highest SRL across all depths for both irrigation regimes followed by *Oryza glaberrima* and Moroberekan, respectively. At 30-60 cm depth, IR64 had over 50% increase in SRL for both irrigation regimes compared at 0-30 cm depth. There was an increase in SRL for all varieties at 60-100 cm for both irrigation regimes with *Oryza glaberrima* having a 50% increment in the control's SRL compared at 30-60 cm depth. Significant increments were also noted in IR64 for the control and Moroberekan for the drought treatment (Figure 3).

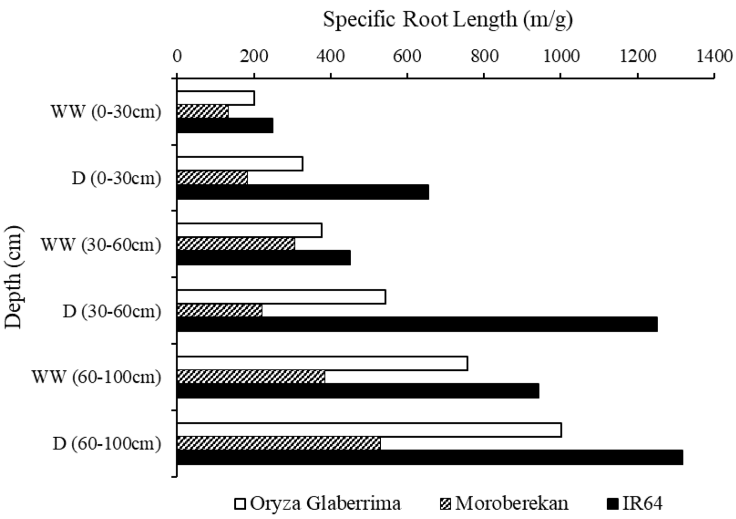


Figure 3. Specific root lengths for all varieties with depth (SED: 217)

Discussion

The high R:S ratio and RWD in the control are due to the availability of soil moisture at FC throughout the duration of the experiment. Soil moisture plays a vital role in root development, nutrient availability and uptake within the rhizosphere (Wu et al. 2005). The production of high shoot biomass during the vegetative stage, which could be remobilised and transferred to grain development as a buffer mechanism to counteract drought effects on yield perhaps caused a reduction in the R:S ratio for the drought treatment. Moroberekan is a tall traditional upland rice variety with a deep thick root system and low tillering ability, which results in high root biomass and low shoot biomass. Usually, a high R:S ratio during drought is due to the development of numerous adventitious roots with high aerenchyma tissues and root osmotic adjustment as plants scavenge for nutrients and reduction in shoot biomass due to early senescence and leaf death. An increase in RWD for Moroberekan and *Oryza glaberrima* at 60-100 cm depth in the drought treatment is related to the plants' response to drought stress to increase root growth to access receding water levels. Root systems subjected to severe water deficit have increased suberisation of existing roots, which results in the production of new roots in deeper soil layers. The even distribution of roots is vital in the acquisition of soil moisture and greater economic return from resource capture (Asch et al. 2005). IR64 has a fibrous shallow root system and mechanical impedance to root elongation during drought reduces root growth at depth.

Soil moisture availability plays a critical role in root growth hence the difference between irrigation regimes at 0-30 cm for RLD. Upland rice varieties established denser root systems than the lowland IR64 at depth. IR64 is characterised by a shallow and fibrous root system with thinner roots in deeper soil layers hence the low RLD. Moroberekan particularly developed numerous lateral seminal roots in addition to the thick nodal roots under drought conditions. Shifts in RLD in deeper soil layers due to drought stress have been highlighted by Price et al. (2002). Aerobic dryland conditions favour root hair formation, which is positively correlated with RLD and SRL (Price et al. 2002). Upland rice varieties tend to develop deep root systems to access receding water levels, a phenological adaptation to their survival. Specific root length correlates with nutrient acquisition capacity of the plant and a high SRL is beneficial under resource deficient situations (Kirkham 2014). The high SRL for IR64 could be attributed to the large fibrous root system within the rhizosphere in comparison with the often fewer and thick roots of upland rice varieties.

Conclusion

Based on their root morphological characteristics, Moroberekan and *Oryza glaberrima* were more drought tolerant compared with IR64. The former two varieties are adapted to upland soil conditions but IR64 modified its root morphology to alleviate the adverse drought effects. Roots are dynamic and express temporal and spatial variability in response to edaphic changes in moisture status and nutrient availability particularly N. However, matching the crop’s phenology to its environment is a keystone of drought tolerance.

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