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Growth, phenological, and yield response of upland rice (*Oryza sativa* L. cv. Nerica 4®) to water stress during different growth stages

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ABSTRACT

Rice (*Oryza sativa* L.) grown in uplands is exposed to variable soil water conditions and unpredictable periods of water stress (WS). The study was conducted to determine the impacts of WS imposed at different phenological stages of upland rice on growth, phenology, recovery of source size, yield and water use efficiency (WUE). The popular cv. Nerica 4® grown in Africa was sown under a rain-out shelter for two seasons. Treatments included a well-watered control (CT) and stress imposed by withholding water for the duration of different stages: tillering (Ti), panicle initiation (PI), anthesis (AT) and grain filling (GF). Name codes used for treatments were thus: CT, STi, SPI, SAT and SGF. When water was withheld, soil water content in the 0–0.6 m soil layer dropped to approximately 50% of plant available water, while stomatal conductance of the abaxial leaf surface and leaf area index decreased significantly, suggesting that severe stress was experienced. Growing degree days to reach the different growth stages were roughly equal in both seasons, even though sowing was in the mid-summer of 2013/2014 and early summer of 2014/2015, respectively. Time to reach peak tillering could not be explained by temperatures and cumulative solar radiation during growth. The onset of reproduction was highly significantly ($p < .0001$) delayed by water stress, independent of whether tiller abortion occurred or not. Findings suggest that lower plant densities are recommended to cope with stress during PI, to reduce water loss and control unproductive tillers at harvest. It is concluded that stress during late reproductive stages, unlike during PI, does not alter crop duration and has a negligible effect on water loss and WUE. Farmers with limited irrigation water can try to avoid WS by making sure they irrigate during PI and save water during later reproductive stages.

1. Introduction

About 11% of the global rice (*Oryza sativa* L.) cultivated area is in uplands (IRRI, 2002). Growing rice in non-puddled, unsaturated and well-drained soils (upland systems) (Kato and Katsura, 2014) is gaining popularity over flooded rice for various merits. This share is likely to increase, particularly because of growing recognition to save water in rice systems (Bouman, 2001; Kato et al., 2006). Growth in rice production and acreage in sub-Saharan Africa (SSA) is estimated at 7% per annum and can be ascribed to the release of improved New Rice for Africa (NERICA®) cultivars (ARC, 2007). These progenies are the result of interspecific crossings between African indigenous upland rice (*Oryza glaberrima* Steud) and Asian lowland rice (*Oryza sativa* L. Japonica) and were developed for low input systems (Jones et al., 1997). The yield of rice in rainfed conditions is comparatively lower in uplands (1.5–2.5 Mg ha^{-1}) than for lowlands (2.5–4.5 Mg ha^{-1}) and approximately 30% lower under similar water supply conditions (ARC, 2007; Kato and Katsura, 2014). This yield difference among Japonica rice cultivars was marginal when water supply was unlimited (Kato et al., 2009), meaning that high potential cultivars need full irrigation. Although water saving technologies, including aerobic systems, have reduced water inputs compared to conventional flooded rice (Tuong et al., 2004), levels of water application are still quite high. The irrigation strategy practiced in aerobic rice systems is to raise soil water content to about field capacity if rainfall is insufficient (Bouman, 2001). Investigations are therefore needed to determine the minimum water requirements for maximum rice productivity.

In most parts of Africa, upland rice is rainfed (Kijoji et al., 2014) and periods of WS are unpredictable due to poor rainfall distribution. Response of rice to WS generally varies with duration, intensity of stress (Heinemann et al., 2011) and most importantly, the growth stage when stress occurs. The three main growth phases

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of rice are the vegetative, reproduction and ripening stages, which are subdivided into 10 principle growth stages (Fageria, 2007), and which overlap even within a single plant because the rice crop makes tillers of different chronological ages. Stress in rice plants was reported to develop at $\Psi_{soil} < -86$ kPa for lowland conditions (Bouman et al., 2001) and at $\Psi_{soil} < -100$ kPa in potted upland soil (Asch et al., 2005), but sensitivity of physiological processes such as transpiration and leaf expansion to WS differs along the crop cycle (Devatgar et al., 2009; Heinemann et al., 2011). Mechanisms to cope with WS in *Oryza sativa* L. are thus well documented for pot, growth chamber and lysimeter studies, although such conditions may not represent field conditions well (Parent et al., 2010; Kijoji et al., 2014). For instance, Ψ_{soil} between −60 and −140 kPa at 0–25 cm depth, which are reported as threshold values for lowland rice growth in anaerobic soils (Bouman et al., 2001), may be atypical of upland conditions; where (i) surface soil can be dryer than −600 kPa (Jensen et al., 1998) and (ii) roots can exploit soil layers deeper than 30 cm (Lilley and Fukai, 1994).

Drought effects on rice growth depends on the timing thereof. Stress between germination and flowering was reported to delay development in lowland and in upland rice (Wopereis et al., 1996; Boojung and Fukai, 1996), but the delay in development was much more pronounced in direct-seeded upland rice compared to transplanted lowland rice (Kijoji et al., 2014). Water stress during the ripening stage reportedly also hastens development (Dingkuhn and Le Gal, 1996). The duration of these phases can also be altered by excess water (Dingkuhn and Asch, 1999) and it remains to be investigated if upland rice is tolerant to some degree of soil saturation. Most studies, such as the one by Boojung and Fukai (1996), did not quantify thermal time, which makes it difficult to assess how sensitive the phenology of upland rice is to WS. Research that generates information on changes in growing degree day (GDD) requirements for different stages under water limited conditions will be useful for optimising crop production systems that entirely depend on rainfall, of which the distribution is usually uneven.

In addition to changes in the duration of different developmental stages, drought affects rice plants in various other ways. Stress between flowering and grain filling increases spikelet sterility (Matsuo et al., 2010), and during panicle initiation (PI) it inhibits panicle exertion (Okada et al., 2002), but Asch et al. (2005) reported that when stressed during vegetative growth, dry matter partioning was not affected. Stress at one stage can also have cumulative effects on subsequent components, for instance tiller abortion with stress during early growth (Wopereis et al., 1996) may reduce panicle number (associated with tiller number) and the final spikelet number per unit area. No investigation considered the duration of developmental stages and demonstrated such effects with WS at all above stages in a single field study. Thus, relative yield loss due to stress during different phenological stages and ideal traits to cope with stress at each growth stage have not been studied well before. With respect to alterations in phenology, it has not been established if delay in flowering under vegetative stress may be a result of new tillers developing after relieve of severe stress (tiller abortion), tiller inhibition without death after mild stress, or due to alteration in dry matter partitioning between plant organs. It is noteworthy that rice tillering is spread over time. Delays in phenology has been related to size of source or canopy, and recovery, dry matter partitioning and growth stage in relation to leaf number (Boojung and Fukai, 1996; Prasertsak and Fukai, 1997; Bouman et al., 2001), with some contrasting reports. An aspect that has not been well reported is whether recovery of source capacity (e.g. canopy size) after stress will be to the same level as for a well-watered control, and whether it will affect the final grain yield. Clarification of source-sink relations is needed since WS during vegetative growth is known to slow development of rice. The crop therefore continues to grow (accumulates dry matter) but at a decreasing rate. It is noteworthy that crop development is different from growth. A crop that has recovered from stress can be of the same canopy size and similar height as a well-watered one, but at a different developmental stage. It is also important to identify desirable traits for yield improvement with stress during different developmental stages in view of variable and cumulative effects of WS on growth and changes after recovery. There is lack of information on effects of drought stress during different developmental stages on phenology (thermal time accumulation), sink-source relations when the stressed crop attains a similar development stage as a well-watered crop, and water use efficiency (WUE). This information is scarce because of a paucity of field studies on WS in rice, especially in unsaturated uplands (Kato et al., 2006), despite the significance of the crop. The overall objective of this study was to determine the effects of water stress on upland rice (cv. NERICA 4®) crop growth and phenology, and to identify the contribution of plant characteristics to yield at each developmental stage. The specific objectives were: (i) to evaluate dry matter partitioning and leaf N content when a crop has recovered from WS, compared to a well-watered control and (ii) to quantify water use and WUE when a rice crop was stressed at different developmental stages.

It is envisaged that this research will inform upland rice growers on best management practices to minimise yield loss under water stress and breeders on traits for adapting rice to water limitations.

2. Materials and methods

2.1. Planting material

Upland rice cultivar NERICA 4® (WAB450-I-B-P-91-HB) (Jones et al., 1997; Ndjiondjop et al., 1998) seed was acquired from the National Crop Resources Research Institute (NaCRRI) in Uganda. Cultivar NERICA 4® is widely adopted in West and East Africa (ARC, 2007) and was chosen because of its high grain yield, estimated at around 4.7 Mg ha^{-1} under rainfed conditions, and because it is still the top-ranked cultivar in tropical rice producing areas such as Uganda (Lamo et al., 2010; Imanywoha et al., 2004). Furthermore, farmers prefer NERICA 4® to other NERICA cultivars for its heavy grains and medium growth duration.

2.2. Study site and rain-out shelter experimental set-up

The trial was conducted in a rain-out shelter on the Hatfield Experimental Farm of the University of Pretoria, South Africa (located at 25° 45′ S, 28° 16′ E and 1370 m a.s.l.), from December 2013 to June 2014 (season 1) and from October 2014 to April 2015 (season 2). The sowing dates are within the planting window of summer crops in South Africa and other parts of SSA. Daily solar radiation, minimum and maximum air temperatures and relative humidity, and wind speed were recorded, and short grass reference evapotranspiration (ETo) was calculated by an automatic weather station located approximately 100 m from the rain-out shelter. Vapour pressure was calculated from relative humidity and temperature. Daily weather parameters during stress periods in the two years are presented in Table 1.

The soil at the site is a deep Hutton (MacVicar et al., 1977), loamy, kaolinitic, mesic, Typic Eutrustox (Soil Classification Working Group, 1991), with an effective depth of 1 m. Soil characteristics over the top 0.6 m depth were: pH (water) 5.8 ± 0.14, 0.5 ± 0.06% C, 4.3 ± 2.4 mg kg^{-1} mineral N, 15.9 ± 11.01 mg kg^{-1} available P (Bray I), 95.6 ± 39.7 mg kg^{-1} K, 1377 ± 48 mg kg^{-1} Ca, 159.8 ± 29.4 mg kg^{-1} Mg, 10.2 ± 1.6 mg kg^{-1} Na, 1400 ± 40 kg m^{-3} dry bulk density, 0.3 ± 0.02 m^3 m^{-3} field capacity, 0.2 ± 0.02 m^3 m^{-3} permanent wilting point, 59.7 ± 1.2% sand, 33.3 ± 2.9% clay and 7.0 ± 2.8% silt. Soil characteristics of the