

Submergence Escape in *Oryza glaberrima* Steud.

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Abstract

Oryza glaberrima, an African monocarpic annual rice derived from *Oryza barthii*, is grown in traditional rice producing wetland areas of West Africa. *Oryza sativa*, an Asian rice that varies from annual to perennial, is derived from *Oryza rufipogon*. Genotypes of *O. glaberrima* are inherently lower yielding than those of *O. sativa* and are, therefore, cultivated in fewer areas. However, because they grow adequately in unstable environments such as those with water stress, they appear to tolerate severe environmental stress. Cultivars of *O. glaberrima* are roughly divisible into two ecotypes: upland and lowland. However, it might be that *O. glaberrima* is a valuable rice species for flooding conditions in all cases. To elucidate the physiological responses of young rice plants to short-term submergence stress, so-called flash flooding, under rainfed conditions for *O. glaberrima* by comparison with several genotypes for lowland adapted, deepwater adapted shoot elongated escape and *Sub1* of *O. sativa*, 30-day-old seedlings were submerged completely for 10 d at 45 cm water depth at 13 d after transplantation in a lowland field. In fact, *O. glaberrima* showed higher shoot elongation ability during submergence than any genotype of *O. sativa* that we tested. However, *O. glaberrima* lodged easily after the end of submergence because of longer and more rapid shoot elongation during submergence. Therefore, it triggered a decrease in its survival rate. On the other hand, various lines of 35 *O. sativa* and 27 *O. glaberrima*, including some classified as short-term submergence tolerant, were compared for submergence tolerance in field and pot experiments to long-term submergence tolerant varieties in other words, deepwater varieties. Submergence-tolerant cultivars of *O. sativa* were unable to survive prolonged complete submergence for 31–37 d, which indicated that the mechanism of suppressed leaf elongation that conferred increased survival of short-term submergence was inadequate for surviving long periods underwater. The superior tolerance of deepwater *O. sativa* and *O. glaberrima* genotypes to prolonged complete submergence appeared to be attributable to their greater photosynthetic capacity developed by leaves that had newly emerged above the floodwater. Cultivars of *O. glaberrima* adapt to long-term complete submergence. Cultivar “Saligbeli” adapted to short to long term submergence.

Keywords: *glaberrima*, lodging, photosynthesis, shoot elongation, submergence escape

Introduction

Rice farming in Africa began approximately 3500 years ago (Porter, 1970). The rice variety cultivated at the time was African rice (*Oryza glaberrima* Steud.), which is native to the continent (Chu and Oka, 1972). African rice is well adapted to the severe local climate, but it has had little opportunity to be improved or selected by humans. It is, therefore, regarded as wild and of low productivity. For that reason, Asian rice (*O. sativa* L.) accounts for a high proportion of the rice consumed in Africa today. However, the development and promotion of a NEw Rice for AfriCA (NERICA) is attracting attention in Africa. Moreover, the properties of African rice, which was employed as a parent strain in the production of NERICA, are now being reassessed. In this manner, rice farming in Africa has been developed differently from that in Asia, and cultivation and cooking methods also differ in many ways. Farmers cultivate rice in irrigated lowlands in Asia,

although rainfed uplands in Africa account for most rice fields. African farmers attach great importance to the quantity immediately after cooking in many cases (Sakagami *et al.*, 2008). Although rice consumption in African countries has shown an increasing trend in recent years, the production rate is not sufficient to meet the demand. The volume of imported rice is increasing annually, which is having a detrimental effect on African countries' economies.

In general, rice cultivation is vulnerable to natural disasters in West Africa. One reason is the shortage of suitable irrigation systems. The area of irrigation is less than 20% of the total area of rice cultivation, and most rice is planted in rainfed regions (Balasubramanian *et al.*, 2007). Therefore, rice cultivation in West Africa is strongly influenced by precipitation or overflow from rivers. However, the status of damage to rice plants by flooding in West Africa has not been understood well until now. Upland rice is severely influenced by rainfall because of the lack of standing water. Yields of upland rice are very low (around 1 t ha⁻¹) compared with those of lowland rice cultivation (around 2 t ha⁻¹) (Norman and Otoo, 2003). Lowlands, therefore, offer greater potential for raising rice production, and represent about 20–50 million hectares, depending on the definition used. At present, only about 10–20% of this area is under cultivation (Africa Rice Center, 2004), thereby offering great potential for rice farming expansion. However, rice plants in lowland areas are often damaged by floods caused by heavy rain. It is, therefore, important to study the effects of submergence on rice plants to develop sustainable rice production in West Africa.

Genotypes of *O. glaberrima* are inherently lower yielding than those of *O. sativa* and are, therefore, cultivated in fewer areas (Linares, 2002). However, because they grow adequately in unstable environments such as those with water stress, they appear to tolerate severe environmental stress. Flooding imposes severe selection pressure on plants, principally because excess water in the plant surroundings can deprive them of certain basic needs, notably of oxygen and of carbon dioxide and light for photosynthesis. It is a major abiotic influence on species' distribution and agricultural productivity world-wide. Based on our analysis, most *O. glaberrima* varieties adapt well when floods are deeper and when they entail long-term submergence in Africa because of their greater photosynthetic capacity developed by leaves that have newly emerged above floodwaters through rapid shoot elongation.

Materials and Methods

Experiment 1: Responses to short-term submergence “flash flood”

To elucidate the physiological responses of young rice plants to short-term submergence stress, so-called flash flooding, under rainfed conditions for *O. glaberrima* by comparison with several genotypes for lowland adapted, deepwater adapted shoot elongated escape and *Sub1* of *O. sativa*, 30-day-old seedlings were submerged completely for 10 d at 45 cm water depth at 13 d after transplantation in a lowland field of Guinea. Dry matter production, plant height, lodging and surviving rate were compared.

Experiment 2: Responses to long-term submergence “deep water”

Various lines of 35 *O. sativa* and 27 *O. glaberrima*, including some classified as short-term submergence tolerant, were compared for submergence tolerance in field and pot experiments to long-term submergence tolerant varieties in other words, deep-water varieties. Plants were submerged completely for 31 d in a field experiment, and partially or completely for 37 d in a pot experiment in a growth chamber. Dry matter production, plant height, leaf area, and photosynthetic rate were compared.

Experiment 3: Flash flood tolerance for cultivated species

Lodging, plant height, and dry matter accumulation for 99 cultivars in *O. sativa*, *O. glaberrima*, and interspecific hybridization progenies (IHP) were measured when 12-day-old

seedlings were submerged completely for 7 d in pots and in fields to make an evaluation of flash flood tolerance.

Results and Discussion

There was a high positive correlation ($P < 0.01$, $r = 0.86$) between shoot length elongation during short term submergence and lodging score at 15 DAS (Day After Submergence) in experiment 1. DRL (Deep-water to Rainfed Lowland genotype in *O. glaberrima*) showed higher shoot elongation during submergence and a higher lodging score after desubmergence than other genotypic groups. On the other hand, ST (Submergence Tolerance genotype) showed the opposite features to DRL with lower shoot elongation and lodging score. RL (Rainfed Lowland genotype), DW (Deep-Water genotype) and SE (Shoot Elongation genotype) showed intermediate traits in shoot length elongation and lodging score between DRL and ST. Figure 1 shows the relationship between shoot length elongation during submergence and survival rate at 19 DAS. There was a negative correlation between shoot length elongation and survival rate ($P < 0.05$, $r = -0.66$).

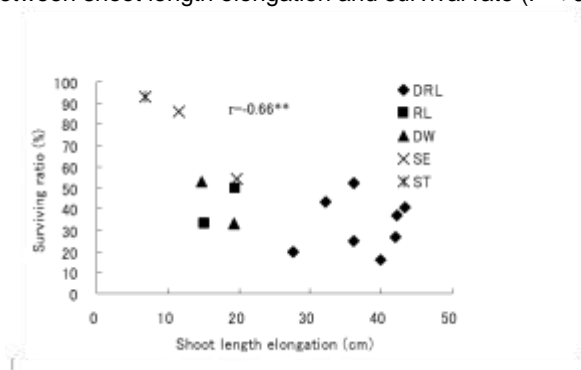
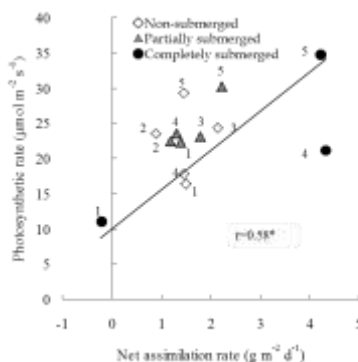


Figure 1. Effect of shoot length elongation on survival rate. Survival rate was calculated for number of plants before submergence divided by number of surviving plants at 19 day after desubmergence

ST of *Sub1* showed the highest survival rate (93%) and the shortest shoot length elongation (6.8 cm) as well as IR 62293- 2B-18-2-2-1-3-2-3 (86%, 11.5 cm) in the SE group. The survival rate of DRL was lower compared with ST. *O. glaberrima* showed higher shoot elongation ability during submergence than any genotype of *O. sativa* tested. However, *O. glaberrima* lodged easily after desubmergence due to longer and rapid shoot elongation during submergence, and thus triggered a decrease in its survival rate. We suggested that *O. glaberrima* was susceptible to short-term submergence while it may be adapted to prolonged flooding because of improved restoration of aerial photosynthesis and survival rate through shoot elongation ability

All cultivars of *O. sativa* with submergence tolerance based on the quiescence strategy failed to regain contact with the aerial environment and died during 31 d submergence in the field experiment 2. In contrast, all *O. glaberrima* genotypes resurfaced and survived submergence. The photosynthetic rates of the youngest fully expanded leaf of the main shoot of pot-grown plants were measured in pot experiment 2. The non-submerged rate for 'IR73020' ($30.9 \mu\text{mol m}^{-2} \text{s}^{-1}$) 1 DBS (Day Before Submergence) was significantly above those for other genotypes. The rate for 'Yele1A' ($6.74 \mu\text{mol m}^{-2} \text{s}^{-1}$) was the lowest. It was, however, significantly greater for Yele1A' than for other genotypes in non-submergence plots ($29.2 \mu\text{mol m}^{-2} \text{s}^{-1}$), in partial submergence plots ($30.3 \mu\text{mol m}^{-2} \text{s}^{-1}$) and in complete submergence plots ($34.8 \mu\text{mol m}^{-2} \text{s}^{-1}$) 37 DAS. The photosynthetic rate at 37 DAS in partial and complete submergence was closely related to the NAR (Net Assimilation Rate) during submergence in the pot experiment (Figure 2).



Symbols represent non-submerged plants, partially submerged plants and completely submerged plants as indicated. The number next to each symbol indicate the cultivars: 1, 'Banjoulou'; 2, 'IR71700'; 3, 'IR73020'; 4, 'Nylon'; and 5, 'Yele1A'

Figure 2. Relationship between net assimilation rate during submergence and photosynthetic rate after 37 d submergence in a pot experiment.

The superior tolerance of deepwater *O. sativa* and *O. glaberrima* genotypes to prolonged complete submergence appears to be due to their greater photosynthetic capacity developed by leaves newly emerged above the floodwater. Vigorous upward leaf elongation during prolonged submergence is, therefore, critical for ensuring shoot emergence from water, leaf area extension above the water surface and a subsequent strong increase in shoot biomass. Increase in shoot DMA after desubmergence was negatively correlated with shoot elongation during submergence, $r = -0.36$ ($P < 0.01$) in experiment 3. ST were plotted in the area of short shoot elongation and high increase in DMA (Dry Matter Accumulation), while *O. glaberrima*, except for Saligbeli, were plotted in the area opposite to that of ST. Some LS (Lowland Sativa genotype) and LI (Lowland Interspecific progenies genotype) were plotted close to the ST for both shoot elongation and shoot DMA. Increase in DMA after desubmergence of all US (Upland Sativa genotype) was less than that of ST.

The first principal component explained 46.8%, and for the classification of cultivars according to their physiological responses to flash floods. The results of the cluster analysis were compared to the principal component analysis results (Figure 3). Principal component analysis was performed with the increase in DMA from 1 DAD to 14 DAD, and lodging at 1 DAD, shoot elongation during submergence, and increased DMA during submergence. In Clusters I, III, and VIII, the main genotypes belonging to each cluster group were classified on the principal component analysis. Cluster I, including ST cultivars, and Cluster VIII, including *O. glaberrima*, were positioned in opposite regions except for Saligbeli. Saligbeli exhibited enhanced shoot elongation with the increase in DMA during submergence. These features seemed to be a unique way to cope with submergence.



Axis I is the first principal component ($y = -0.403942 x_1 + 0.434866 x_2 + 0.329416 x_3 - 0.271996 x_4$). Axis II is the second principal component ($y = -0.068947 x_1 - 0.080874 x_2 + 0.618871 x_3 + 0.722613 x_4$), x_1 , x_2 , x_3 and x_4 represent increase in DMA after desubmergence, lodging score, shoot elongation and increase in DMA during submergence respectively. All data are standardized. (●) Upland Sativa, (○) Lowland Sativa, (▲) Upland Glaberrima (△) Lowland Glaberrima, (■) Upland IHP, (□) Lowland IHP, (x) Submergence tolerance.

Figure 3. Principal component analysis of the physiological traits linked to submergence (shoot elongation during submergence, increase in dry matter accumulation during submergence, lodging score and increase in dry matter accumulation after desubmergence).

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