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Growth Responses of Seedlings in *Oryza glaberrima* Steud. to Short-term Submergence in Guinea, West Africa

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Abstract

In inundation areas in rainfed lowland and inland valleys of Guinea as well as other regions in Africa, submergence for a few days to a few weeks with a water depth less than 50 cm occurs in rice cultivation during the rainy season. Young rice seedlings after transplanting are particularly vulnerable to submergence stress. *Oryza glaberrima* Steud. is well adapted to growth in inundation areas with deepwater conditions in West Africa; however, it is not evident whether it resists short-term submergence stress after transplanting. The purpose of the study was to understand the physiological responses of rice plants after transplanting to short-term submergence stress under rainfed conditions for *O. glaberrima* by comparison with several genotypes of *Oryza sativa* L. from Guinea. Eight genotypes of *O. glaberrima* and seven genotypes of *O. sativa* including two shoot elongation genotypes, one submergence tolerant genotype as a control cultivars, and four genotypes of common cultivars in West Africa were used. Thirty day-old seedlings were submerged completely for 10 days with medium deepwater conditions at 45 cm water depth at 13 days after transplanting in a lowland field. *O. glaberrima* showed higher shoot elongation ability during submergence than any genotype of *O. sativa* that we 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. The submergence tolerant genotype of *O. sativa* maintained the dry matter weight of the leaf blade during submergence through the inhibition of shoot elongation. We suggest that *O. glaberrima* is susceptible to short-term submergence while it may adapt to prolonged flooding because of improved restoration of aerial photosynthesis and survival rate through shoot elongation ability.

Discipline: Crop production
Additional key words: anaerobic conditions, dry matter, leaf expansion, shoot elongation, survival

Introduction

Shallow, submergence-prone lands are generally favorable for rice production except that they are subject to unpredictable, short-term submergence that may damage the crop, especially when flooding occurs soon after transplanting[10]. Moreover, excess water triggers serious damage to the growth and survival rate of rice[11,12]. Flood conditions differ in duration and water depth. Therefore, different morphological or physiological traits are required to adapt to each environment[3]. Setter et al.[15] described that elongation ability is required in areas where the water depth generally exceeds 50 cm for more than 14 days in order to resume aerobic metabolism. On the other hand, many non-elongation-of-shoot cultivars during submergence show tolerance to short-term submergence for a few days or weeks[17]. One of the adverse factors of shoot elongation is an increase in carbohydrate consumption for cell division, cell elongation and maintenance of the elon-

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gated shoot[5,17,19]. Therefore, reduced carbohydrate metabolism during submergence is important for short-term submergence tolerance[7]. Tolerance is a physiological adaptation, whereby the plant can change metabolic pathways to adapt to the submergence environment; meanwhile, avoidance is a morphological adaptation, whereby the plants can avoid stress conditions to keep metabolic pathways in normal conditions[2].

In West Africa, about 40% of the cultivated area is rainfed lowland. In coastal areas, the inundation areas in lowland and inland valleys of Guinea, submergence often lasts for a few days to a few weeks with a water depth of less than 50 cm during the rainy season. Young rice seedlings after transplanting are particularly vulnerable to submergence stress. *Oryza glaberrima* Steud. adapts well in inundation areas with deepwater conditions in West Africa[4]. Deepwater rice is usually flooded deeper than 50 cm for one month or longer during the growing season. Futakuchi et al.[2] demonstrated that the chlorophyll content of the leaf blade and photosynthetic O_2 evolution rate of *O. glaberrima* were maintained more strongly than those of *O. sativa* L. under deepwater conditions. *O. glaberrima* also showed higher shoot elongation than *O. sativa*. In the light of this evidence, it is reasonable to suppose that *O. glaberrima* has higher resistance to deepwater stress. Although limited research has been carried out into the physio-morphological responses to deepwater of *O. glaberrima,* little is known about their submergence tolerance to short-term submergence stress after transplanting. The purpose of this study is to investigate how *O. glaberrima* responds to short-term submergence stress compared to *O. sativa* after transplanting in rainfed lowland in Guinea.

Materials and methods

Eight genotypes of *O. glaberrima* and seven genotypes of *O. sativa* were examined (Table 1). In *O. glaberrima* (DRL), five genotypes were from Mali, two from Guinea and one genotype from Senegal, and these genotypes are adapted to deepwater to rainfed lowland. In *O. sativa*, one submergence tolerant genotype (ST) and two shoot elongation genotypes (SE) were donated from the International Rice Research Institute, two genotypes adapted to deepwater (DW) were from Mali and two genotypes adapted to rainfed lowland (RL) from Guinea[13]. Submergence tolerance is the ability of rice plants to survive 10–14 days of complete submergence and renew its growth when the water subsides with no stem elongation during submergence[3,5,15]. The shoot elongation type increases plant length by the elongation of internodes, leaf sheaths, leaf blades, or a combination of these.

Rice seedlings were transplanted in the experimental lowland field of Foulaya Agricultural Research Center in the Republic of Guinea (10º 0′ N, 12º 9′ W) at 17 days after seeding with 121 hills (11 × 11) for the individual genotypes at a density of 16.7 hills m^{-2} (30 cm × 20 cm) and two replicates. The paddy soil was Ferralsols, and characterized as a sandy soil. The pH of the soil was 4.2 before transplanting. Rice plants were flooded completely at 13 days after transplanting for 10 days at a 45 cm water depth. The flooded water was very muddy during the submergence. The water level was kept at 2 cm depth before and after flood treatment. Floodwater in the experiment field was drained continuously during the flooding. The water temperature was measured at four corners at a 30

Table 1. List of genotypes examined in the experiment

Species	Abbreviation name	Genotypic group	Genotype	Origin[a)]
O. glaberrima	DRL	Deepwater to rainfed lowland	Alyba	Mali
	DRL	Deepwater to rainfed lowland	Bagua Kandie	Mali
	DRL	Deepwater to rainfed lowland	CG14	Senegal
	DRL	Deepwater to rainfed lowland	Gbagaye	Mali
	DRL	Deepwater to rainfed lowland	Salifore	Guinea
	DRL	Deepwater to rainfed lowland	Saligbeli	Guinea
	DRL	Deepwater to rainfed lowland	Simo Bareo	Mali
	DRL	Deepwater to rainfed lowland	Simo Boro	Mali
O. sativa	DW	Deepwater	Bouba Moussa	Mali
	RL	Rainfed lowland	CK21	Guinea
	RL	Rainfed lowland	CK40	Guinea
	DW	Deepwater	Gorbal	Mali
	SE	Shoot elongation	IR62293-2B-18-2-2-1-3-2-3	IRRI
	SE	Shoot elongation	IR72431-5B-18-B-10-1	IRRI
	ST	Submergence tolerance	IR67520-B-14-1-3-2-2	IRRI

a): Origins include an organization.

cm depth in the morning (9:00), noon (12:00) and evening (16:30). The averages of water temperature during the day for 10 days submergence were from 25.6ºC to 33.1ºC.

The timing of each measurement was described as the number of days from the day of beginning the submerged treatment. The plant length of five plants was measured in the field using a 50 cm ruler at one day before submergence (DBS), and 11, 29 and 46 days after submergence (DAS). The leaf area of five plants was measured using an automatic area meter (AAM-9, Hayashi Denko Co. Ltd.) at 14 DBS, 1 DBS and 11 DAS. The leaves (leaf blade) and stems (culm + leaf sheath) of five plants were harvested and dried in an oven for 48 hours at 80ºC to measure the dry matter weight at 14 DBS, 1 DBS and 11 DAS. The degree of lodging at 5 days after the water level receded (15 DAS) was scored from 1 (no-lodging) to 5 (complete lodging). The survival rate was calculated through the evaluation of plants growing with green leaves at 19 days after the water level receded (29 DAS).

Results

1. Shoot elongation

Figure 1 shows the changes of plant length during the experiment from 14 DBS to 46 DAS (36 days after water receded) for each genotypic group. The submergence treatment was performed for 10 days. The average plant length before submergence was 24.9 cm to 32.1 cm in all the genotypic groups. In all the groups except for ST, the top leaf reached to the water surface during submergence. The plant length of DRL was the lowest at 1 DBS among all the genotypic groups, while it was the highest at 11 DAS. DRL increased in length rapidly during submergence compared to the other genotypic groups in *O. sativa*. A significant difference in plant length was recognized between DRL and the other genotypic groups at 11 DAS at $p < 0.01$. The averages for shoot length elongation during submergence of DRL, RL, DW, SE, and ST were 37.5, 17.4, 17.0, 15.6, and 6.8 cm, respectively. All the genotypic groups except for ST decreased plant length because of the death of elongated leaves after the water level receded to 29 DAS.

2. Leaf area and dry matter production

Dry matter weights of leaf blades and stems at 14 DBS, 1 DBS and 11 DAS of the genotypic groups are shown in Fig. 2. All the genotypes increased in total dry

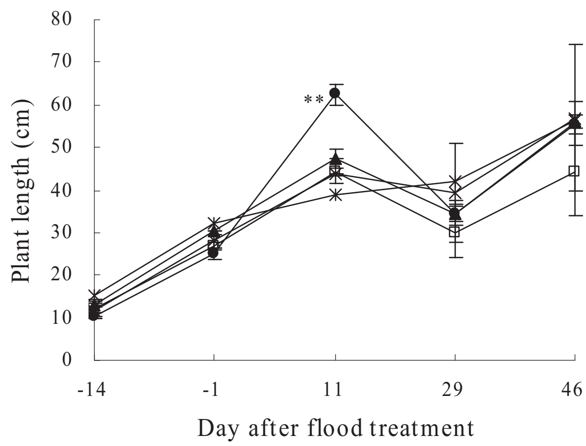

Fig. 1. Change in plant length during the experiment
●:DRL; Deepwater and rainfed lowland rice in *O. glaberrima,* □:RL; Rainfed lowland rice in *O. sativa,* ▲:DW; Deepwater rice in *O. sativa,* ×:SE; Shoot elongation rice in *O. sativa,* ⁎:ST; Submergence tolerance rice in *O. sativa.* The vertical bars indicate standard deviation of the means of ten plants.

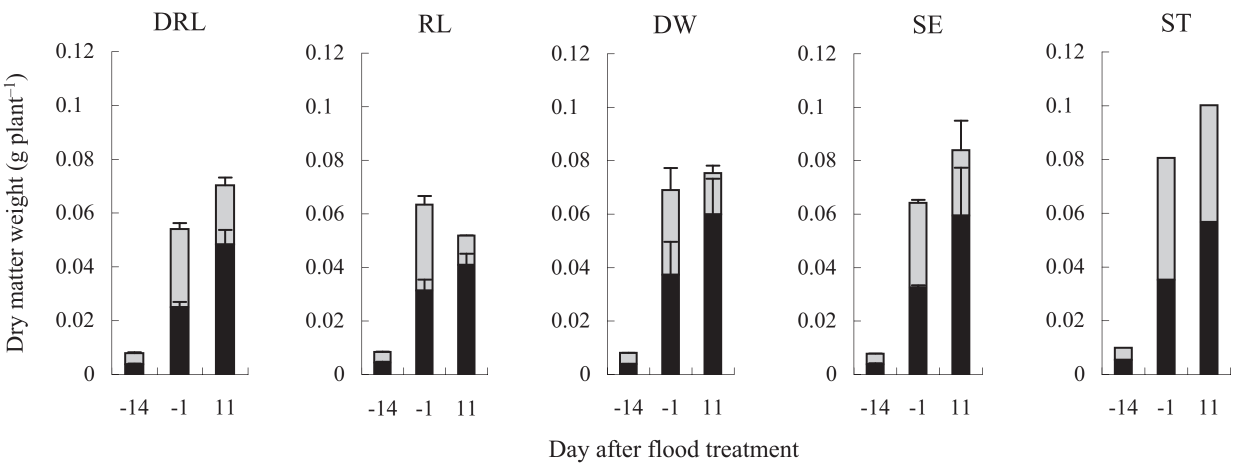

Fig. 2. Change in dry matter weight of leaf blade and stem before and after desubmergence
Vertical error bars indicate a standard deviation among genotypes except for ST.
□: Leaf blade, ■: Stem.

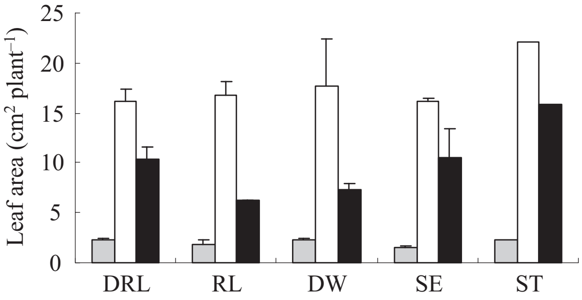

Fig. 3. Change in leaf area before and after desubmergence
Vertical error bars indicate a standard deviation among genotypes except for ST.
□: 14 DBS, □: 1 DBS, ■: 11 DAS.

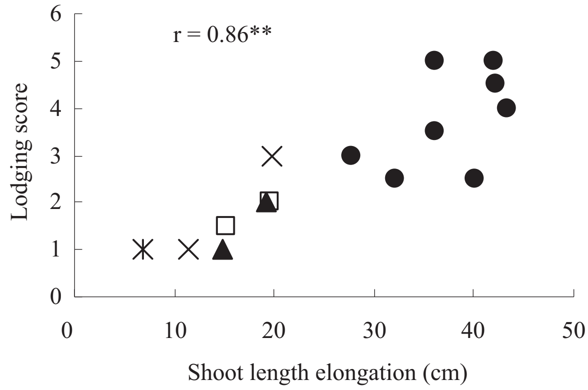

Fig. 4. Relationship between shoot length elongation during submergence and lodging after desubmergence
●:DRL; Deepwater and rainfed lowland rice in *O. glaberrima,* □:RL; Rainfed lowland rice in *O. sativa,* ▲:DW; Deepwater rice in *O. sativa,* ×:SE; Shoot elongation rice in *O. sativa,* ⋇:ST; Submergence tolerance rice in *O. sativa.*

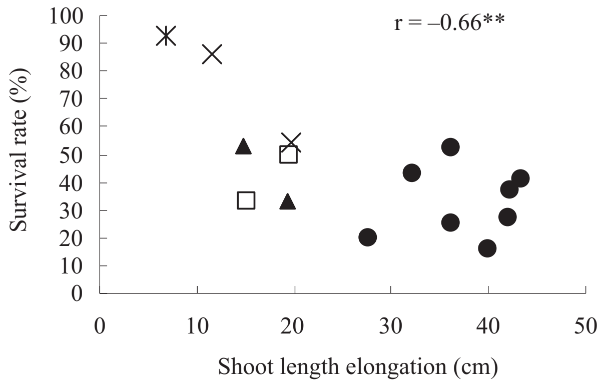

Fig. 5. Relationship between shoot length elongation during submergence and survival rate after desubmergence
Survival rate is calculated for number of plants before submergence divided by number of surviving plants at 19 day after desubmegence.
●:DRL; Deepwater and rainfed lowland rice in *O. glaberrima,* □:RL; Rainfed lowland rice in *O. sativa,* ▲:DW; Deepwater rice in *O. sativa,* ×:SE; Shoot elongation rice in *O. sativa,* ⋇:ST; Submergence tolerance rice in *O. sativa.*

matter weight of shoots between 1 DBS and 11 DAS except for RL. The total dry matter weight at 11 DAS was the largest in ST, and the smallest in RL. The partitioning of the dry matter weight of stem to total dry matter weight during submergence was changed due to the genotypic group. The partitioning of the dry matter weight of stem to total dry matter weight before and after submergence was 46.3% and 68.8% in DRL, 49.4% and 78.8% in RL, 54.0% and 79.4% in DW, 50.9% and 70.8% in SE, and 43.6% and 56.6% in ST.

The leaf area decreased at 11 DAS compared to 1 DBS in all the genotypic groups (Fig. 3). In particular, in RL (–63.1%) and DW (–58.6%) the leaf area decreased much more during submergence by the calculation of the decrease ratio [(1 DBS-11 DAS)/1 DBS] in the leaf area, compared to DRL (–36.2%), SE (–35.2%) and ST (–28.3%). Leaf area at 1 DBS and 11 DAS was the largest in ST. There was a significant positive correlation ($r = 0.97$, $P < 0.01$) between dry matter weight of the leaf blade and leaf area at 14 DBS, 1 DBS and 11 DAS.

3. Lodging and plant survival

There was a high positive correlation ($P < 0.01$, $r = 0.86$) between shoot length elongation during submergence and lodging score at 15 DAS (Fig. 4). DRL showed higher shoot elongation during submergence and a higher lodging score after desubmergence than other genotypic groups. On the other hand, ST showed the opposite features to DRL with lower shoot elongation and lodging score. RL, DW and SE showed intermediate traits in shoot length elongation and lodging score between DRL and ST. Figure 5 shows the relationship between shoot length elongation during submergence and survival rate at 29 DAS. There was a negative correlation between shoot length elongation and survival rate ($P < 0.05$, $r = –0.66$). ST 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 genotype group. The survival rate of DRL was lower compared with ST.

Discussion

All the genotypes showed shoot length elongation during submergence for 10 days with a 45 cm water depth in the paddy field, and DRL had the highest shoot elongation ability (Fig. 1). The average shoot length elongation of DRL during submergence was 2.2-, 2.2-, 2.4- and 5.5-fold greater than that of RL, DW, SE and ST, respectively, in *O. sativa*. The results concur with those of Futakuchi et al.[2] who pointed out that *O. glaberrima* shows higher shoot elongation ability than *O. sativa* under flooding conditions. The results suggest that DRL has different traits to any of the genotypes of *O. sativa* that we tested for shoot elongation responses to short-term submergence stress after transplanting in rainfed lowland in Guinea. SE did not elongate its stem much during submergence similar to the RL and DW genotypes. It may be presumed that the shoot elongation ability relates to the submergence period and growth stage of rice. A characteristic of SE is internode elongation during submergence, but the internode elongation does not start at an early growth stage after transplanting[18], and was not observed in this experiment.

In the case of short-term submergence, the recovery of plant growth after the water level recedes is also important[5]. All the genotypes except for ST showed the death of elongated leaves. The leaves that elongated during submergence lodged after the water level receded, which resulted in death. Another reason may be the failure of physiological adaptation to the environmental change from anaerobic to aerobic conditions. In general, oxidative stress is a serious problem for survival in aerobic conditions; therefore, the plants have to contain mechanisms for adequate protection from oxidative stress[1]. However, the plants damaged by flooding cannot rapidly initiate their protection systems after the water level recedes[8,9]. ST showed the highest survival rate, suggesting that ST has a good ability to adjust to the environmental changes in this experiment.

Mazaredo and Vergara[11] showed that submergence tolerant genotypes tended to have greater leaf areas with higher carbohydrate and nitrogen contents during submergence compared to susceptible genotypes. In this experiment, ST had the highest leaf area and dry matter weight of the leaf blade and stem after desubmergence among the genotypes analyzed (Fig. 3). Growth and photosynthetic responses of lowland rice following complete submergence are related to the concentration of CO_2 dissolved in floodwater[14]. Low CO_2 concentrations do not only reduce photosynthesis, but they also lead to adverse interactions with high concentrations of ethylene[6]. We concluded that it is not evident whether submergence tolerance depends on the increase of shoot biomass during submergence. Although shoot elongation during complete submergence competes with maintenance processes for energy and carbohydrates[16], if the leaves can come into contact with the air as a result of shoot elongation, rice plants may maintain their shoot growth such as dry matter weight and leaf area. We focus attention on the partitioning of dry matter weight between the leaf blade and stem during submergence. The dry matter weight in the stem increased in all the genotypes, while those in the leaf blade decreased except for ST during submergence. Most of the genotypes concentrated the dry matter weight to the stem during submergence to support shoot elongation with a resulting decrease in leaf area. It was found through the field experiment that ST maintains the dry matter weight of leaf blades during submergence through the inhibition of shoot elongation. Keeping dry matter weight in the leaf blade during submergence may support recovery growth after the water level recedes, by the maintenance of carbohydrate supply. However, maintaining the dry matter weight is difficult for long-term complete flooding, because of the limitation of photosynthetic activity underwater. From this viewpoint, shoot elongation ability to return to aerobic growth conditions is needed for long-term flood survival. DRL can grow by rapid shoot elongation during submergence after transplanting. However, DRL lodges easily after desubmergence due to its elongated shoot resulting in a decreased survival rate (Fig. 5). A further important point is that there is a close relationship between shoot length elongations less than 20 cm and the survival rate. Most of the genotypes in DRL survived as well as DW and RL while the elongation of DRL was mostly larger than 28 cm. DRL exhibits rapid growth characteristics of shoot elongation during submergence, which is an important issue for growing DRL in regions prone to submergence for prolonged periods, due to its improved ability to restore aerial photosynthesis and produce an improved survival rate.

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