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Submergence Tolerance of Rice Species, *Oryza glaberrima* Steudel

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1. Introduction

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* (Sakagami et al., 1999). 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. Strong submergence-induced elongation is a widespread escape mechanism that helps submerged plants regain or retain contact with the aerial environment on which they depend (Arber, 1920). This mechanism enables plants to resume anaerobic metabolism and photosynthetic fixation of CO₂ by raising their shoots above water. Escape strategies based on elongation by stem or leaves are prominent characteristics of deep-water and floating rice. However, rapid elongation by leaves of young plants in response to short-term submergence flash flood (for up to 2 weeks) adversely affects tolerance by depleting carbohydrates that would otherwise support survival during and after submergence (Chaturvedi et al., 1995; Setter & Laureles, 1996; Kawano et al., 2002; Ram et al., 2002; Jackson & Ram, 2003; Joho et al., 2008). The submergence tolerance gene, *Sub-1A*, depresses shoot elongation under short-term submergence to ensure survival. Submergence-tolerant rice varieties tend to accumulate more starch in their stem section than susceptible varieties do. They experience less carbohydrate depletion after submergence (Karin et al., 1982; Emes et al., 1988). To improve the circumstances of tolerant plants to survive under flooding conditions is a major constraint for sustainable agriculture in unstable environments undergoing climate change. Consequently, in this chapter, we describe physiological mechanisms related to photosynthesis on submergence tolerance for rice species that are widely cultivated in West Africa.

2. Physiological mechanism on flooding tolerance in rice species

Kawano (2009) showed that suppression of underwater elongation brought about by the mutated form of *Sub-1A* in *O. sativa* is beneficial for the endurance of complete

submergence. Consequently, non-shoot-elongation-cultivars during submergence show tolerance to short-term submergence, so-called flash flooding, for a few days or weeks. Sakagami et al. (2009) emphasized that this trait is inappropriate when selecting and breeding cultivars of *O. sativa* or *O. glaberrima* in cultivated rice for resilience to longer term submergence. Under these circumstances, a vigorous ethylene-mediated underwater elongation response by leaves is necessary to return leaves to air contact and full photosynthetic activity for long-term complete submergence.

2.1 Anaerobic metabolism in submerged rice plants

The rate of gas exchange is very slow in water because of small diffusion coefficients for gases (oxygen, $0.201 \text{ cm}^2 \text{ s}^{-1}$ in air; $2.1 \times 10^{-5} \text{ cm}^2 \text{ s}^{-1}$ in water) (Armstrong, 1979). When water becomes stagnant, the oxygen concentration becomes especially low at night because of the nighttime respiration of algae. Rice plants increase the rate of alcoholic fermentation under low oxygen environments. However, alcoholic fermentation produces only two molecules of ATP per glucose molecule, which is not efficient when compared with aerobic respiration, through which 32 molecules of ATP are produced per glucose molecule. Therefore, rice cannot survive in a low oxygen environment for a long period because of the shortage of carbohydrates in the rice plants for use in energy production. Furthermore, photosynthesis is limited by low irradiance when the plant is submerged. It is necessary to improve photosynthetic capacity and the effective use of photosynthetic products as well as to survive under water.

Strategy	Quiescence		Escape
Submergence tolerance	Slowing of ethylene-promoted leaf elongation to conserve energy	Rapid leaf elongation	Rapid internodal or stem elongation to resume anaerobic metabolism and photosynthesis
Ecological adaptation	Flash floods less than two weeks	Short-term submergence (Shallow-water)	Long-term submergence (Deep-water)
Gene expression(e.g)	<i>SUB1A</i>	<i>SUB1C</i>	<i>SNORKEL1, 2</i>
Carbohydrate consumption	Low (limited by <i>Sub1A</i>)	High	High

Table 1. Strategy by submergence tolerance of rice

Rice has adapted to submergence-prone environments through the use of two strategies (Table 1): submergence tolerance to flash floods where a rapid increase in water level causes partial to complete submergence for up to 2 weeks, and shoot elongation to short to long term submergence. *Sub1A* gene in *O. sativa* reportedly confers submergence tolerance to flash floods through a quiescence strategy in which cell elongation and carbohydrate metabolism in young seedlings is repressed during submergence (Fukao et al., 2006). This strategy is a predominant tolerance mechanism that is driven by adjustment of metabolism.

A strategy with shoot elongation shows two different mechanisms: rapid shoot elongation in shallow floods in a short-term submergence and internodal or stem elongation in deep water in long-term submergence. Based on our analysis, most *O. glaberrima* varieties adapt well when floods are deeper and when they entail long-term submergence (Fig. 1). These mechanisms for plant survival under submergence are affected by the conservation of energy and carbohydrate accumulation (Perata et al., 2007).



Fig. 1. Growing rice of *O. glaberrima* along the Niger River in Niger

2.2 Submergence tolerance with elongation for deep water

Rapid shoot elongation for young seedlings is usually disadvantageous in conditions of short-term submergence with deep water conditions because lodging usually occurs once floodwaters recede. This water regime adapts well, using submergence tolerance with a quiescence strategy. By tolerance, cell elongation and carbohydrate metabolism are repressed. Furthermore, fast shoot elongation can restore contact between the leaves and air, but it can also result in death if carbohydrate reserves are depleted before emergence in leaves above the water surface. Leaf elongation during submergence is controlled by the interaction of at least three plant hormones: ethylene, GA, and ABA (Kende et al., 1998). Accumulated ethylene is probably the primary signal which triggers the plant to start a cascade of reactions leading to enhanced cell elongation (Voesenek et al., 2006) because ethylene is accumulated in rice plants during submergence because of the fact that gas diffusion is 10^4 -fold slower in solution than in air (Armstrong, 1979). The cascade model was proposed from the study of stem elongation in deepwater rice (Kende et al., 1998).

2.2.1 Submergence escapes mechanism with shoot elongation

Rapid elongation of the leaves and leaf sheath is advantageous for rainfed lowland varieties because it enables them to avoid submergence stress when moderate flooding occurs during the early vegetative stage. Deepwater rice is often characterized as floating rice. Nevertheless, the differences in characteristics of floating rice and deepwater rice remain unclear. In fact, the physiological mechanisms of growth differ between the two. Some rice

plants can survive and stand without floating in water at 1 m water depth. In this chapter, such rice plants that stand without floating in water are designated as deepwater rice to distinguish them from floating rice. In general, the plant height of deepwater rice reaches 140–180 cm in the absence of submergence (Catling, 1992), but the abilities of deepwater rice shoots to extend are varied. Deepwater rice can maintain an aerobic metabolism during submergence via development of its canopy above water because of the elongation of its internodes and because of its long leaves. Deepwater rice's ability to elongate in a single day is less than that of floating rice. However, deepwater rice can adapt to submergence under conditions in which the water level increases 5 cm per day (Catling, 1992). However, this type of tall plant architecture often causes lodging after the water recedes.

2.2.2 Internode elongation

Setter et al. (1988) demonstrated that the adverse effects are caused mainly by reduced photosynthesis capacity because of CO₂ starvation in the shoot organs during submergence. Furthermore, they suggested a relation between ethylene concentration, leaf chlorosis and leaf elongation. Partial submergence treatment to deep water rice never affects carbohydrate and sugar contents in newly developed leaves under the water compared to the control (Setter et al., 1987). Elongation with floating ability is the most important morphological feature of deepwater rice. In particular, internode elongation is a more important mechanism for increasing shoot length. Internode elongation is related closely to plant hormones. Submergence lowers the O₂ level in rice internodes. Then low O₂ levels simulate ethylene synthesis. Ethylene accumulation occurs in the submerged internodes. Then high internodal ethylene concentration increases the sensitivity of tissues to gibberelic acid or increases the concentration of physiologically active gibberellins, thereby leading to commonly observed growth responses (Rose-John & Kende, 1985). Deepwater rice differs in its ability to accumulate carbohydrate contents within the cultivar's carbohydrate content, which does not correlate with the total internode length or plant length (Vergara et al., 1975).

3. Flooding response of *O. glaberrima*

O. glaberrima, a monocarpic annual derived from *O. barthii* (Sakagami et al., 1999), is grown in traditional rice production in the wetlands of West Africa. It is highly adapted to deepwater inundation in countries such as Gambia, Guinea, Mali, Niger, Senegal, and Sierra Leone in West Africa (Inouye et al., 1989). The first gene pool of *O. glaberrima* was inferred as an inland delta of the Niger River because of the high gene diversity among species. In Guinea, for example, coastal or lowland areas are heavily affected by submergence during the rainy season. Rice plants are often partially or completely submerged for more than a month. Such prolonged submergence often triggers crop failures. Guinea's farmers prefer to cultivate *O. glaberrima* fields with prolonged submergence because of such advantageous traits as those explained above. 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. Tolerance of other abiotic and biotic stress such as drought (Maji et al., 2010), rice yellow mottle virus (Thiemele et al., 2010), African rice gall midge (Nwilene et al., 2009), and iron toxicity (Majerus et al., 2007) has been found in some cultivars of *O. glaberrima*. However, it is vulnerable to NaCl salinity (Awala et al., 2010),

grain shattering (Koffi, 1980), and lodging (Dingkuhn, 1998). It is reasonable to presume that the indigenous cultivated species of African rice can provide useful genes for improvement of tolerance to major stress in Africa.

3.1 Responses to short-term submergence “flash flood”

The flooding response of *O. glaberrima* should be discussed thoroughly, but it is not clear from Futakuchi’s report (2001) whether shoot elongation contributes to flooding tolerance in different water regimes or not. 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 (Joho et al., 2008). 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 (Fig. 2).

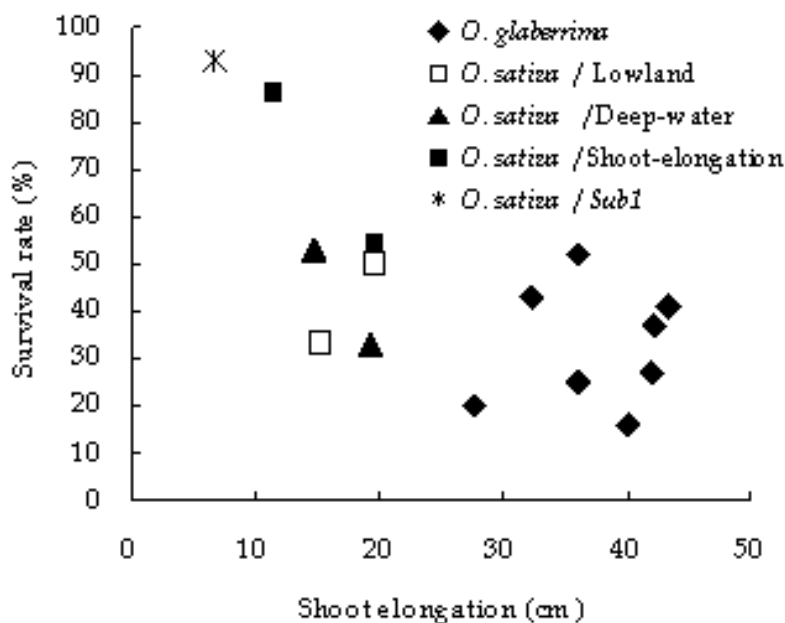


Fig. 2. Effect of shoot elongation during submergence on survival rate after desubmergence. Survival rate is observed at 14 d after desubmergence.

The submergence-tolerant genotype (*Sub1*) of *O. sativa* maintained the dry matter weight of the leaf blade during submergence through the inhibition of shoot elongation using the quiescence strategy, thereby attaining a survival rate of 93%. The escape strategy for *O. glaberrima* is therefore the effective usage of stored carbohydrates for shoot elongation in a severely photosynthesis-limited environment. However, failure to regain contact with air and the oxygen, carbon dioxide, and light it supplies invariably gives rise to severe carbohydrate depletion. Therefore, this escape strategy carries a high risk for young rice plants (Kawano et al., 2009). We reported that *O. glaberrima* is susceptible to short-term submergence, although it might adapt to prolonged flooding because of improved restoration of aerial

Genotype	Non-submergence		Complete-submergence	
	Shoot elongation (cm d ⁻¹)	Shoot biomass increase (g d ⁻¹)	Shoot elongation (cm d ⁻¹)	Shoot biomass increase (g d ⁻¹)
<i>O. sativa</i> L.				
BA8A	1.38	0.41	1.78	0.04
Balante	0.94	0.34	1.17	0.02
Banjoulou	0.95	0.32	1.23	0.02
Cinquant-deux	1.25	0.55	2.12	0.16
CK20	1.45	0.37	1.58	0.03
CK211	1.32	0.40	1.82	0.04
CK4	1.31	0.33	1.49	0.03
CK41	1.52	0.41	1.71	0.04
Danta rouge	1.54	0.48	2.43	0.07
EH-IA-CHIU	1.16	0.42	1.39	0.02
FR13A*	1.19	0.38	Death	Death
Gallale Blanc	0.65	0.24	1.89	0.12
Haira koreye	1.43	0.45	2.15	0.05
IR49830-7-1-2-2	0.97	0.40	1.40	0.02
IR62293-2B-18-2-2-1-3-2-3	1.59	0.47	1.61	0.04
IR67520-B-14-1-3-2-2*	1.01	0.35	Death	Death
IR70027-8-2-2-3-2*	1.50	0.46	Death	Death
IR71700-247-1-1-2	1.19	0.42	1.65	0.02
IR73018-21-2-B-2-B*	0.95	0.35	Death	Death
IR73020-19-2-B-3-2B*	1.32	0.29	Death	Death
Kaolac	1.23	0.36	1.60	0.03
Kaorin	0.99	0.42	1.55	0.02
Köticondre	1.03	0.49	1.42	0.03
Marsal	1.09	0.45	1.72	0.05
N 22	1.26	0.43	1.69	0.05
N'ckrome	0.97	0.46	1.70	0.04
NIK 1A	1.17	0.53	1.30	0.02
Nylon	1.18	0.32	1.58	0.02
Protocolo	1.47	0.41	2.10	0.04
Reymont	1.03	0.22	1.21	0.01
ROK21	1.22	0.20	1.60	0.03
SHAI-KUH	1.08	0.38	1.29	0.03
Vandana	1.46	0.41	1.65	0.03
WAR1(ROK22)	1.26	0.32	1.58	0.03
Wonsongg orgle	0.88	0.26	1.53	0.02
<i>O. glaberrima</i> Steud.				
Aawba	1.14	0.32	1.84	0.08
Bakin Iri	1.06	0.51	1.87	0.12
CG14	0.97	0.40	1.67	0.07
Dam Iri	1.25	0.57	2.02	0.16
Dembou bourawana blanc	0.75	0.18	1.99	0.09
Djéifata noir	0.96	0.36	2.25	0.11
Djingua noir	0.76	0.35	1.91	0.14
Douboutou II	0.91	0.36	1.89	0.07
Gbagaye	1.10	0.34	1.95	0.06
Gbobaye	1.13	0.46	1.87	0.06
Kossa barkaneye	1.26	0.44	1.96	0.11
Mala Noir II	0.99	0.31	2.08	0.13
Mala Noir III	0.89	0.32	2.24	0.16
Mogo	1.28	0.47	2.24	0.14
Mokori	1.05	0.36	2.25	0.10
Pegnesso	0.71	0.23	2.06	0.07
RAM23	0.70	0.44	2.13	0.14
Salifore	1.39	0.49	1.80	0.08
Saligbeli	1.23	0.38	2.00	0.10
Salikutaforé	1.14	0.30	1.68	0.04
Samandényi	1.08	0.20	1.62	0.07
Sukéré	1.42	0.42	1.90	0.15
Tierka banc	0.91	0.31	2.06	0.13
Tombobokéri II	1.25	0.30	1.95	0.11
W0492	1.87	0.49	1.87	0.06
Wana thireye	1.25	0.42	2.06	0.13
Yélé 1A	0.63	0.32	1.96	0.17
Average(±SE)				
<i>O. sativa</i> L.(n=30)	1.20±0.04	0.39±0.02	1.63±0.05	0.04±0.01
<i>O. glaberrima</i> Steud.(n=27)	1.08±0.05	0.37±0.02	1.97±0.03	0.10±0.01
<i>O. sativa</i> x <i>O. glaberrima</i>	NS	NS	**	**

*Genotypes are characterised by *Sub1*

Table 2. Effect of submergence to shoot elongation and biomass in the field experiment

photosynthesis and survival rate through shoot elongation ability. Enhancement of shoot elongation during submergence in water that is too deep to permit re-emergence by small seedlings represents a futile escape strategy that is used at the expense of existing dry matter in circumstances where underwater photosynthetic carbon fixation is negligible. Consequently, it compromises survival or recovery growth once floodwater levels recede and plants are exposed again to the aerial environment. Consequently, shoot elongation capability to revert to anaerobic growth condition is vital for long-term flood survival.

3.2 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, deepwater varieties (Sakagami et al., 2009). 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. Leaf elongation and growth in shoot biomass during complete submergence in the field were significantly greater in *O. glaberrima* than in *O. sativa* (Table 2).

Submergence-tolerant cultivars of *O. sativa* were unable to survive prolonged complete submergence for 31–37 d, which indicates that the mechanism of suppressed leaf elongation that confers increased survival of short-term submergence is inadequate for surviving long periods underwater. The *O. sativa* deepwater-adapted cultivar ‘Nylon’ and the ‘Yele1A’ cultivar of *O. glaberrima* succeeded in emerging above the floodwater. The photosynthetic rate was higher in deeply submerged plants than in non-submerged plants. The photosynthetic rate at 37 d after submergence in partial and complete submergence was closely related to the net assimilation rate during submergence (Fig. 3), which caused greatly increased shoot length, shoot biomass and leaf area, in association with an increased net assimilation rate compared with the lowland-adapted *O. sativa* ‘Banjoulou’.

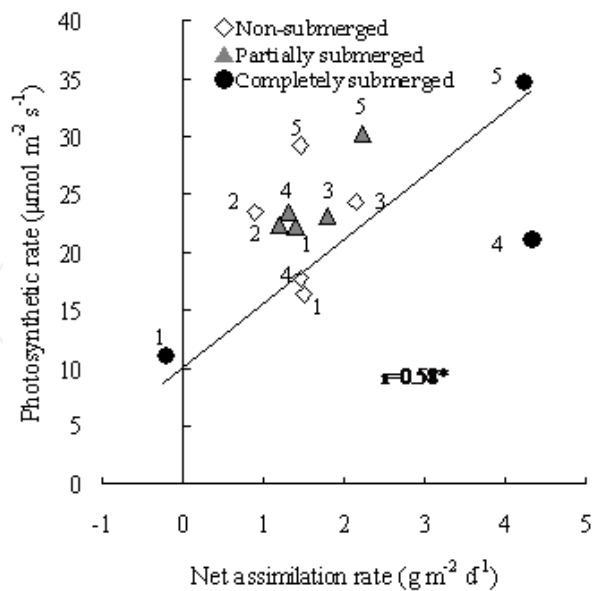


Fig. 3. Relationship between net assimilation rate during submergence and photosynthetic rate after 37 d submergence in a pot experiment. The number next each symbol indicates the cultivars: 1, Banjoulou; 2, IR71700; 3, IR73020; 4, Nylon; 5, Yele1A. Net assimilation rate indicates the increase of dry weight per unit area during 37 d submergence.

The superior tolerance of deepwater *O. sativa* and *O. glaberrima* genotypes to prolonged complete submergence appears to be attributable to their greater photosynthetic capacity developed by leaves that had newly emerged above the floodwater. Vigorous upward leaf elongation during prolonged submergence is therefore critical for ensuring shoot emergence from water, as are leaf area extension above the water surface and a subsequent strong increase in shoot biomass.

Actually, 'Ye1A' had an especially large capacity for shoot elongation when submerged. Watarai and Inoue (1998) noted that high internodal elongation contributes to shoot elongation using *O. glaberrima* under flooding regimes. Faster shoot elongation of *O. glaberrima* genotypes underwater is mainly caused by leaf elongation, but not internodal elongation. Consequently, internode and leaf elongation underwater share certain similarities in *O. glaberrima*, both presumably being stimulated by ethylene.

3.3 Unique physiological mechanism to complete submergence of "Saligbeli"

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 for 7 days in pots and in fields. Upland rice (*O. sativa*) showed greater shoot elongation, greater reduction in dry matter accumulation during submergence, and higher lodging, which indicate low flash flood tolerance. The physiological traits of most *O. glaberrima* and upland rice (*O. sativa*) for resistance against flash flooding were opposite those of submergence-tolerant cultivars, as evidenced from the results of a principal component analysis (Fig. 4). Axis I is the first principal component.

$$Y = -0.403942x_1 + 0.434866x_2 + 0.329416x_3 - 0.271996x_4 \quad (1)$$

Axis II is the second principal component.

$$Y = -0.068947x_1 - 0.080874x_2 + 0.618871x_3 - 0.772613x_4 \quad (2)$$

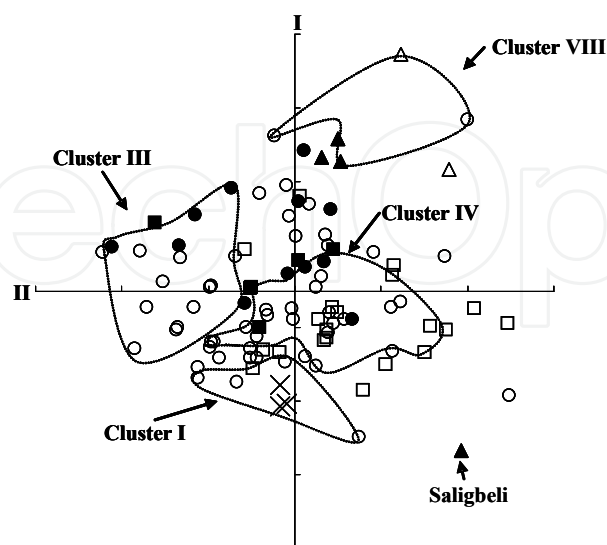


Fig. 4. Principal component analysis of physiological traits linked to submergence. (●)Upland *sativa*, (○)Lowland *sativa*, (▲)Upland *glaberrima*, (△)Lowland *glaberrima*, (■)Upland IHP, (□)Lowland IHP, (×) Submergence tolerance(*Sub1*)

x_1 , x_2 , x_3 and x_4 in (1), (2) represent in dry matter accumulation after desubmergence, lodging score, shoot elongation and increase in dry matter accumulation during submergence respectively. It is accounted for 74.0% of the total number of genotypes with the first and second principal components.

In Cluster I, III, and VIII, the main genotypes belonging to each cluster group were classified on the principal component analysis. Cluster I, including submergence tolerance genotype, and Cluster VIII, including *O. glaberrima*, were positioned in opposite regions.

The physiological response of Saligbeli cultivar differed from those of other *O. glaberrima* genotypes in terms of submergence tolerance. Saligbeli was found by the author in coastal regions in Guinea. Saligbeli exhibited enhanced shoot elongation with increased dry matter accumulation after the end of submergence, as was found also for the submergence-tolerant cultivar in a pot experiment (Table 3). The difference between pot and field experiments might be attributable to different characteristics of the submergence environment, such as turbidity. These features of Saligbeli were apparently a unique means to cope with submergence. These experiments revealed that enhancement of shoot-elongation during submergence are accomplished using dry matter of leaves that had developed before submergence.

Species	Geniotype	Shoot elongation (cm) ¹⁾	Increase of DMW (mg plant ⁻¹)		Ratio of DMA ²⁾	Lodging score ³⁾
			During submergence (7d)	After desubmergence (14d)		
<i>O. glaberroma</i>	Aawba	16.6	-6.4	-18.2	0.18	3
	Saligbeli	12.1	13	59.2	0.99	2
	Samandenyi	15.1	-3.2	-4.0	0.34	6
	Sedou Bayebeli	13.2	-2.0	-19.9	0.12	6
	CG14	19.5	2.6	0	0.30	6
	DouboutouII	34.6	-8.6	-21.4	0.07	6
<i>O. sativa (Sub1)</i>	IR70027-8-2-2-3-2	3.1	4.0	31.0	0.99	1
	IR73020-19-2-B-3-2B	1.2	6.0	23.2	0.98	1
	IR49830-7-1-2-2	4.6	2.4	26.8	0.84	1

1) Increase of plant height during submergence, 2) Ratio of dry matter accumulation (DMA) was determined by dividing the submergence in the control, and 3) Score 7 is the highest and 1 is the lowest in lodging degree after desubmergence.

Table 3. Physiological traits linked to submergence tolerance in *O. glaberrima* and *O. sativa* of *Sub1*

4. Conclusion

Submerged rice is in an anaerobic environment because of the 10⁴-fold slower gas diffusion underwater than in air. Furthermore, levels of oxygen, and carbon dioxide and light for photosynthesis drastically differ according to the floodwater period, depth, temperature, and turbidity. African rice, *O. glaberrima* can lodge readily under aerobic conditions after desubmergence because of weakening of the shoot base, which causes rapid leaf elongation and which increases plant mortality through photosynthetic products accumulated before submergence is exhausted under short-term submergence with the rapid increase of water level: so-called flash flooding. However, cultivars of *O. glaberrima* adapt to long-term

complete submergence apparently because of their greater photosynthetic capacity developed by leaves that have newly emerged above floodwaters through rapid shoot elongation. The Saligbeli cultivar of *O. glaberrima*, with its unique physiological mechanisms, is apparently well-adapted to both conditions for short and prolonged submergence. It therefore holds promise as a selecting and breeding rice genotype for use in different flood-prone regions in Africa.

5. Acknowledgment

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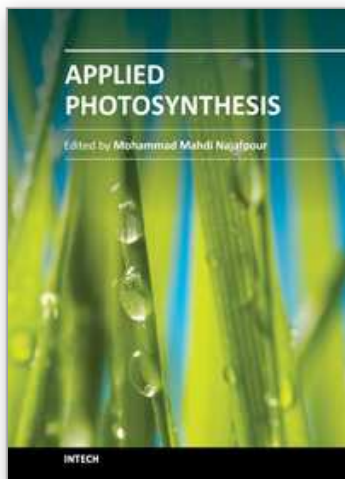
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