Relationship between Shoot Elongation and Dry Matter Weight During Submergence in *Oryza sativa* L. and *O. glaberrima* Steud. Rice Cultivars

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**Abstract**: Rice plants are damaged by flash floods with a rapid increase in water level caused by a heavy rain. However, rice plants cope with the flash floods either by an “escape strategy” involving rapid shoot elongation or by a “quiescence strategy” involving surviving under water with minimal activity. As we found in previous experiments, Saligbeli cultivar adapted well to flash floods through rapid shoot elongation. To understand the vigorous growth process during submergence, we studied the relationship between shoot elongation and changes in dry matter weight (DMW) during submergence. *O. glaberrima* Steud. cv. Saligbeli and *O. sativa* L. cv. Ballawé and IR 49830-7-1-2-2 were used. Saligbeli and Ballawé exhibit shoot elongation, and IR 49830-7-1-2-2 exhibits flash-flood tolerance due to the presence of the *Sub-1* gene. Twelve-day-old seedlings were submerged for 7 days and the plant length and DMW were measured. The plant length ratio of submerged to control plants in Saligbeli was higher than that of other cultivars during 2-6 days of submergence but IR 49830-7-1-2-2 shoot elongation was inhibited by submergence. In all three cultivars, the elongation of the developing leaf sheath conferred shoot elongation during submergence. The plant length of all submerged plants showed a strong positive correlation with DMW of the leaves developed during submergence. Submerged Saligbeli and Ballawé showed strong negative correlations between DMW of the leaves developed before and during submergence (*r* = –0.786 for Saligbeli and –0.772 for Ballawé, *P* < 0.05), suggesting that the enhancement of shoot elongation during submergence is accomplished by using dry matter of the leaves developed before submergence. However, the correlation was not observed in the submerged IR 49830-7-1-2-2. Further details from studies using isotopes are also needed to understand the plant growth during submergence.

**Key words**: African rice, Flash floods, Flood tolerance, *Oryza glaberrima*, *Oryza sativa*, Shoot elongation, *Sub-1*, Submergence.

Rice planting starts at the beginning of the rainy season in most parts of Guinea, West Africa. The rice ecosystem there involves rainfed lowlands that depend completely on rainfall or ground water for water supply, which varies greatly with the area and year, with occasional heavy rain causing rice seedlings to be submerged. Rice plants under such conditions are affected by two major topography-dependent factors, water depth and submergence period. Farmers use older seedlings for transplanting and the leaves about 50 cm high to prevent water inflow from flooding in Guinea. In such leved rice fields, water flooded into the fields remains stagnant due to poor drainage, sometimes submerging seedlings for long periods. In the fields without boundaries, flash floods rapidly increase water depth, but then recede within several days. Considering strategic options to lessen plant stress, the ideal rice cultivar should be tolerant to temporary submergence (flash-flood tolerance) or should have rapid elongation ability, or both. In our previous screening of flash-floods, using the broad genetic resources of *O. sativa*, *O. glaberrima*, and interspecific hybridization progenies, Saligbeli (*O. glaberrima*) had tolerance to flash-floods due to good adaptation to anaerobic conditions with rapid shoot elongation (Kawano et al., 2008).

The two general types of flash-flood resistance are flash-flood tolerance and elongation ability. Most rice cultivars die within several days under complete submergence, but some cultivars such as FR 13A, are highly tolerant to flash floods, and survive complete submergence for around 2 weeks. Tolerance of FR 13A is conferred by a major quantitative trait locus designated as *Sub-1* gene on chromosome 9 (Xu and Mackill, 1996; Siangliw et al., 2003; Xu et al., 2006). Physiological traits of cultivars with the *Sub-1* gene include strong flash-flood tolerance in different locations and over different years (Mazaredo and Vergara, 1982; Jackson et al., 1987; Adkins et al., 1990; Chaturvedi et al., 1995), suggesting that the genetic inheritance of flash-flood tolerance is applicable to a wide range of regions. The major morphological and physiological flash-flood tolerance traits indicated elsewhere (Setter et al., 1997; Ito et al., 1999; Ram et al., 2000).
al., 2002; Jackson and Ram, 2003) include slow leaf elongation, slow chlorosis, high carbohydrate reserve storage during submergence, and quick adaptation to aerobic environments after desubmergence. Given the above traits, carbohydrate metabolism during submergence seems to be the most important factor in flash-flood tolerance, and the “quiescence strategy” is characterized by slow growth that conserves energy and carbohydrates (Perata and Voesenek, 2007).

Elongation during submergence, an “escape strategy,” enables rice plant to resume aerobic metabolism by raising their shoots above the water surface. The escape strategy of rice plants adapts to deepwater and floating rice areas, where submergence with a greater than 50 cm water depth continues for more than one month. However, in short-term submergence rapid leaf elongation adversely affects flash-flood tolerance (Jackson, 1985; Chaturvedi et al., 1995; Setter and Laureles, 1996; Kawano et al., 2002; Ram et al., 2002). Both lodging after desubmergence (Ito et al., 1999) and increase in carbohydrate consumption for cell division, cell elongation, and maintenance of elongated leaves (Setter and Laureles, 1996; Ito et al., 1999; Voesenek et al., 2006) are adverse factors of the leaf elongation strategy. Leaf elongation and carbohydrate metabolism are thus closely related to flash-flood tolerance. The negative relationship between flash-flood tolerance and shoot elongation during submergence was confirmed using 903 cultivars from the IRRI gene bank collection (Setter and Laureles, 1996). However, the effect of shoot elongation on carbohydrate metabolism and dry matter weight (DMW) remains poorly understood.

Yamada (1959) reported that rice plants lost starch and carbohydrates from leaves and roots during submergence. The amount of carbohydrate present during submergence correlates positively with flash-flood tolerance (Palada and Vergara, 1972; Emes et al., 1988; Chaturvedi et al., 1995; Mallik et al., 1995) and is determined by the balance between consumption and supply, so shoot elongation increases carbohydrate consumption (Voesenek et al., 2006), starving carbohydrates of submerged plants. Photosynthesis, which is important in supplying carbohydrates and O2 for aerobic respiration, depends on CO2 and irradiation during submergence (Setter et al., 1989), and is generally inhibited by submergence. CO2 for photosynthesis is also limited in water due to its low absolute concentration compared with O2; air-saturated water contains 0.288 mol m⁻³ O2 but only 0.011 mol m⁻³ CO2 at 25°C and it diffuses only slowly through the inevitable boundary layer (Jackson and Ram, 2003). Lower irradiance also inhibits photosynthesis under water (Setter et al., 1987). Cultivars such as Saligbeli show flash-flood tolerance by rapid shoot elongation (Kawano et al., 2008). The physiological mechanisms of vigorous growth during submergence improve both flash-flood tolerance and deep-water resistance in Africa. We studied the relationship between shoot elongation and DMW during submergence to understand the vigorous growth of submerged rice plants.

Materials and Methods

Experiments were conducted at the Foulaya Agricultural Research Center (10°0'N, 12°9'W) in the Republic of Guinea from May to June, 2006, using Saligbeli (Oryza glaberrima Steud.), Ballawé, and IR 49830-7-1-2-2 (O. sativa L.). Saligbeli and Ballawé are local cultivars from Guinea, and IR 49830-7-1-2-2 (IR 49830) is a flash-flood tolerant cultivar containing the Sub-1 gene. Seeds were soaked for 3 days at room temperature in the dark as a pre-germination treatment. Five pre-germinated seeds were sown in 0.58 L plastic pot filled with dried paddy field soil. Rice plants were grown without a fertilizer, and thinned to one plant per pot at 7 days after sowing. Twelve-day-old seedlings at the 4.2-leaf stage for Saligbeli and 5.0-leaf stage for Ballawé and IR 49830 were submerged in a 5,130 L outdoor concrete tank filled with water to the depth of 1 m. The seedlings were submerged completely for 7 days. The average distance between the top of the plants and water surface immediately after submergence was 77.8 cm for Saligbeli, 64.5 cm for Ballawé, and 72.0 cm for IR 49830, and after 7 days submergence was 51.5 cm for Saligbeli, 46.9 cm for Ballawé, and 68.2 cm for IR 49830. The same rice cultivars were planted in the concrete tank without submergence as controls.
Environmental conditions during submergence were as follows: the average water temperature at a 70 cm water depth was 30.2°C during the day, and mean irradiation at 50 cm above the water surface at 1200 during submergence was 1401 μmol m⁻² s⁻¹ photosynthetic active radiation (PAR).

The shoot length of three plants for each cultivar was measured inside the tank, and the same samples were measured throughout the experiment. Three plants of each cultivar were harvested from 3 pots before submergence and each day during submergence. Plants were divided into 4 parts: roots, culms plus leaf sheaths, leaf blades, and dead leaves. All samples were oven-dried at 80°C for at least 48 hours, and DMW was measured using an electronic balance.

**Results**

1. **Shoot elongation**

Fig. 1 shows changes in plant length during submergence. Saligbeli and Ballawé enhanced shoot elongation during submergence. The plant length of Saligbeli was 22.2 ±0.4 cm before submergence, but increased to 45.0 ±1.4 cm after 7 days of submergence, showing 1.39 times more rapid growth in the submerged treatment than in the control (Table 1). The plant length of Ballawé was 35.5 ±0.6 cm, and the tallest of all the cultivars, before submergence. Submerged Ballawé elongated their shoots, to a length of 53.1 ±1.6 cm after 7 days of submergence corresponding to 1.22 times higher growth than that in the controls (Table 1). On the other hand, the plant length of IR 49830 was 28.0 ±0.6 cm before submergence and 31.8 ±0.2 cm after 7 days of submergence, which was 0.86 times that of the controls (Table 1). The shoot elongation rate per day in the submerged Saligbeli was higher than that in the control plants from day 1 to 3. The elongation of the submerged Saligbeli during day 1 to 2 under submergence was 11.5 ±0.3 cm, which was significantly greater than that of the control plants and other submerged cultivars (P <0.01). After 4 days of submergence, the elongation rate per day in the submerged Saligbeli was similar to or less than that in the controls. Submerged IR 49830 did not show a higher shoot elongation rate than the control plants.

Table 1 shows the mean difference of leaf length at each leaf position between submerged and control plants at day 7 of submergence.

| Cultivar | 1st | 2nd | 3rd | 4th | 5th | 6th | 7th |
|----------|-----|-----|-----|-----|-----|-----|-----|
| Saligbeli| 1.01| 1.33| 1.45| 1.51| 1.51| 1.45| 1.39|
| Ballawé  | 1.05| 1.10| 1.11| 1.20| 1.19| 1.19| 1.22|
| IR 49830-7-1-2-2 | 0.97| 0.97| 0.96| 0.93| 0.91| 0.89| 0.86|

* and ** indicates significant differences between control plants and submerged plants at the levels of P < 0.05 and P <0.01 respectively.
leaf blade of Saligbeli over the control plants, but the submerged plant did not develop the 6th leaf sheath within 7 days after submergence, so the 6th leaf length did not exceed that of the 5th leaf length. The fifth leaf sheath elongation contributed to greater shoot elongation of the submerged Saligbeli. The leaf age of Ballawé was around the end of the 5th leaf stage at the beginning of submergence, and the submerged Ballawé elongated the 5th leaf sheath until 2 days after submergence. Ballawé increased the elongation of the 6th leaf sheath at a higher rate than the control plants from days 2 to 5 after submergence. The elongation rate of the 6th leaf blade in submerged plants was similar to that in the control plants. Leaf blade and leaf sheath elongation in IR 49830 cultivars was similar in both submerged and control plants except for the 7th leaf blade length at days 5-7 after submergence. The youngest leaf sheath was developed in control plants, but not in the submerged plants within 7 days of submergence.

2. Dry-matter weight

Fig. 3 shows the changes in whole-plant DMW (shoots and roots) during submergence. DMW increased in all control plants except for days 2-3 in all cultivars and days 4-5 in Ballawé. The DMW of submerged plants showed no significant difference among cultivars during days 1-6 under submergence. DMW of Ballawé was 83.3 ± 6.9 mg, which was lighter than that of IR 49830, 103.0 ± 6.3 mg, and of Saligbeli, 122.7 ± 13.3 mg, after 7 days of submergence.

Fig. 4 shows the DMW change of the leaves developed before submergence (2nd, 3rd, 4th leaves and 5th leaf blade) and those developed during submergence (5th leaf sheath and, and the 6th and 7th leaves). The DMW of the leaves developed during submergence was significantly lighter than that in the control plants at 7 days after the start of submergence (P<0.05 in Saligbeli and IR 49830, P<0.01 in Ballawé). In Saligbeli and IR 49830, DMW
of the leaves developed before submergence did not show significant differences between the submerged and control plants, but in Saligbeli, it was lighter in the submerged plants than in the control from days 2 to 7 of submergence. In submerged Ballawé, DMW of the leaves developed before submergence was significantly lighter than that in the control plants after 7 days of submergence treatment (P < 0.05).

Analysis of the relationship between plant length and whole-plant DMW, showed strong positive correlations between plant length and DMW in the control plants (Fig. 5 A). The correlation coefficient of the controls was 0.914 in Saligbeli, 0.866 in Ballawé, and 0.956 in IR 49830 (P < 0.01). Saligbeli and Ballawé did not show significant correlation coefficients in submerged plants, i.e., 0.390 in Saligbeli and 0.101 in Ballawé. In contrast, submerged IR 49830 showed a strong correlation at r = 0.815 (P < 0.05). Fig. 5 B shows the relationship between the plant length and DMW of the leaves developed before submergence treatment. The control plants of Saligbeli and Ballawé did not show any strong relationship, but IR 49830 showed a negative correlation at r = -0.726 (P < 0.05). On the other hand, the submerged Saligbeli and Ballawé showed a strong negative relationship with r = -0.755 in Saligbeli and -0.741 in Ballawé (P < 0.05). However, the correlation coefficient in IR 49830 was -0.525, and did not show a strong negative relationship. Fig. 5 C shows the relationship between plant length and DMW of the leaves developing during submergence. Both the control and submerged plants showed a strong positive relationship. However, control plants in all cultivars showed higher linear regression coefficients than the submerged plants, except for IR 49830. Fig. 5 D shows the relationship between DMW of the leaves developed before submergence and that during submergence. The submerged Saligbeli and Ballawé showed a strong negative relationships with r = -0.786 in Saligbeli and -0.772 in Ballawé (P < 0.05). The correlation coefficient in IR 49830 was -0.632, and did not show a significant correlation.

**Discussion**

Flash flood resistance is accomplished by rice cultivars in two ways—(1) flash-flood tolerance by quiescence, e.g., in IR 49830, and (2) escape from submergence by leaf elongation to reach above the water level, e.g., in Saligbeli and Ballawé. In shoot elongation, Saligbeli is more adaptable than Ballawé due to faster and more extensive shoot elongation. Aerobic plants depend on the supply of oxygen from their environment to support respiration for energy production and other life-sustaining oxidation and oxygenation for maintaining basic metabolism, meaning that most aerobic plants cannot survive for more than a few days without oxygen (Vartapetian and Jackson, 1997). When plants are submerged, they change energy metabolism from aerobic respiration to fermentation due to the shortage of oxygen (Dolferus et al., 1994). Alcoholic fermentation is not as effective as aerobic respiration for energy production and thus consumes much more carbohydrate than aerobic respiration in plant growth and maintenance, causing depletion of carbohydrate reserves. This means that rice plants must raise their leaves above the water surface as soon as possible and recover aerobic respiration for efficient energy production. Saligbeli showed rapid shoot elongation upon submergence, which is an important physiological trait in shoot-elongation cultivars. *O. glaberrima* is a cultivated species of rice that was first domesticated in the inland Niger River delta around 1500 BC by indigenous inhabitants in the area (Portères, 1970). More recently, *O. glaberrina* has been replaced by *O. sativa*, which has a higher grain yield (Linares, 2002).
Even so, it is still cultivated in flood-prone areas of the Niger River (Sakagami, 1995), since *O. glaberrima* has high adaptability to submergence and deep-water environments. Futakuchi et al. (2001) examined the physiological responses of *O. glaberrima* (CG 14, CG 20, TOG 5810, and TOG 6283) to submergence, and found that *O. glaberrima* promoted shoot elongation following submergence and had higher photosynthetic activity than *O. sativa* during submergence.

The plant length of Ballawé was the largest among the three cultivars used here before submergence, and although the shoot elongation was less than that of Saligbeli, it remained larger than Saligbeli during submergence. Thus, Ballawé is planted in deepwater areas in Guinea, and the tall stature of Ballawé confers an advantage in maintaining aerobic growth conditions.

On the other hand, shoot elongation was inhibited by submergence in IR 49830, which showed typical *Sub-1* gene traits. This phenomenon is called a “quiescence strategy”. Carbohydrate consumption is minimized by inhibiting shoot elongation, which is an excellent strategy for survival. CO₂ is a limiting factor in underwater photosynthesis mainly due to its extremely low solubility in water compared to O₂, and diffusion through the inevitable boundary layer is slow (Jackson and Ram, 2003). Lower irradiance also inhibits underwater photosynthesis (Setter et al., 1987). Therefore, increasing the carbohydrate supply to the plant is not expected under water.

 Shoot elongation during submergence, particularly in short-term submergence such as flash-floods, is thought to have an adverse effect on flash-flood tolerance due to wasted carbohydrates and lodging after desubmergence (Jackson, 1985; Chaturvedi et al., 1995; Setter and Laureles, 1996; Kawano et al., 2002; Ram et al., 2002). However, the effect of the shoot elongation on carbohydrate metabolism during submergence has not been studied extensively. In this study, we focused on the relationship between the shoot elongation and DMW.

Shoot elongation in all submerged cultivars is observed only in the leaf sheath developed during submergence, meaning that one of the effects of submergence is specific to this organ. In control plants, DMW increased during shoot elongation, but in submerged plants DMW did not change during submergence though the shoot elongates (Fig. 3). Submerged Saligbeli and Ballawé cultivars did not show significant correlations between whole-plant DMW and the plant length during submergence (Fig. 5 A). However, both cultivars showed strong positive correlations between the plant length and DMW of the leaves developed during submergence (Fig. 5 C), meaning that the carbohydrate must be supplied to the parts developing during submergence.
from other sources within the plant. Control plants of Saligbeli and Ballawé did not show any significant correlation between DMW of the leaves developed before and during submergence (Fig. 5 D). However, the submerged plants in both cultivars showed strong negative correlations between DMW of the leaves developed before and during submergence (Fig. 5 D), suggesting that a part of the DMW of the leaves developed during submergence in Saligbeli and Ballawé, is supplied from the leaves developed before submergence. On the other hand, in submerged IR 49830, which did not increase shoot elongation during submergence, no significant correlation was observed between DMW of the leaves developed before submergence and shoot elongation (Fig. 5 B) or between the DMW of developed leaf and developing leaves (Fig. 5 D), suggesting that DMWs of the leaves developed before submergence is not used by the leaves developed during submergence. Therefore, in shoot elongating cultivars the enhancement of shoot elongation ability during submergence may be supported by the dry-matter allocation from leaves developed before submergence. Further detailed experiments using isotopes are needed for the study of dry-matter allocation during submergence.

Submergence-adapted plants appear to survive effectively under water by adequate morphological and metabolic changes. *Rumex palustris*, for example, increases the angle of the youngest petioles horizontally (Cox et al., 2003), hyponastically changing petiole orientation from prone to almost vertical, decreasing the distance between the leaf blade and water surface (Voesenek and Blom, 1989; Banga et al., 1997). The flood-tolerant maize cultivar teosinte grows roots adventitiously at the soil surface during flooding to absorb oxygen (Mano and Omori, 2007). Most plant strategies in the face of submergence are related to energy metabolism. Shoot-elongation rice cultivars recover aerobic respiration and maintain low carbohydrate consumption. Flash-flood-tolerant cultivars keep carbohydrate consumption low by inhibiting shoot elongation. Although their response to submergence differs, the common strategy of retaining carbohydrates for energy production and survival during submergence results in flash-flood resistance.

**Conclusion**

There are two strategies for flash-flood resistance, the quiescence strategy and the escape strategy. The physiological characteristic of the quiescence strategy is the inhibition of shoot elongation during submergence. The shoot elongation of submerged and control plants in IR 49830 cultivars correlated positively with whole-plant DMW. However, the growth during submergence was less than that under aerobic conditions, which confers low carbohydrate consumption.

On the other hand, the physiological characteristic of the escape strategy is the enhancement of leaf sheath elongation of the leaves developing during submergence. Submerged Saligbeli and Ballawé cultivars did not show significant correlations between whole-plant DMW and the shoot elongation during submergence, suggesting that shoot elongation is not accompanied by a subsequent input of dry matter sources. However, DMW was increased in organs elongating during submergence. Saligbeli and Ballawé showed strong negative correlations between the shoot elongation and DMW of the leaves developed before submergence, suggesting that DMW of the leaves developed before submergence is used for the leaf elongation during submergence. This is one of the strategies for the vigorous growth under the photosynthesis-limited conditions.

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