Physiological and Morphological Mechanisms of Submergence Resistance in African Rice (Oryza glaberrima Steud.)

Koichi FUTAKUCHI, Monty P. JONES * and Ryuichi ISHII

Graduate School of Agricultural and Life Sciences, University of Tokyo, Tokyo, 113-8657 Japan
* West Africa Rice Development Association (WARDA), 01 B.P. 2551 Bouaké 01, Côte d’Ivoire

Abstract Four Oryza glaberrima lines were characterized with respect to the mechanism of physiological tolerance and morphological avoidance of submerged conditions compared to two O. sativa varieties. The two O. glaberrima lines (TOG 5810 and TOG 6283) were deep water ecotypes, and the other two (CG 14 and CG 20) were upland ecotypes. Under overhead flooding conditions, all the O. glaberrima lines showed a higher photosynthetic O2 evolution rate and chlorophyll content than Normn 30, an O. sativa subspecies of japonica type, while IR36, an O. sativa subspecies of indica type, showed a photosynthetic rate and chlorophyll content almost as high as those of the O. glaberrima lines. Moreover, the O. glaberrima lines displayed higher elongation rates than the O. sativa varieties under submerged conditions. These findings indicated that O. glaberrima exhibited mechanisms of tolerance and avoidance of submergence, suggesting that O. glaberrima could be a genetic source for the breeding of deep water varieties. No clear difference was observed in the level of tolerance and avoidance of submergence between deep water and upland ecotypes of O. glaberrima.

Key words Oryza glaberrima Steud., Oryza sativa L., Photosynthesis, Stem elongation, Submergence tolerance, West Africa

Introduction

West Africa is characterized by highly diverse environments for rice cultivation, encompassing all the major ecosystems: irrigated lowland, upland, rainfed lowland, deep water areas and mangrove swamps, as indicated in the classification of the International Rice Research Institute3). Deep water area accounts for 6% of the whole rice growing area in West Africa2, mainly in the flood plains of large rivers like the Niger river19), where sudden flood destroys the rice plants. Besides, rice plants sometimes experience submergence damage after excessive rainfall in rainfed lowland areas, which often occurs in inland valley bottoms. The rainfed lowland areas account for 20% of the total rice cultivated areas and 47% of the lowland rice areas in West Africa3). Therefore, submergence is considered to be one of the serious constraints on rice cultivation in this sub-region.

African rice (O. glaberrima Steud.), a domesticated rice species indigenous to West Africa, is still being cultivated, though Asian rice (Oryza sativa L.) is now popular in West Africa. Particularly, African rice is widely cultivated in the Sokoto Rima river flood plains where deep water fields prevail12). Therefore, based on the conditions of cultivation in West Africa, it is considered that O. glaberrima is a plant species resistant to submergence. When O. glaberrima was grown under deep water conditions, elongation of the stem was considered to be the mechanism for the avoidance of submerged conditions in some O. glaberrima lines of floating types8,16). However, little information is available.

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about the physiological aspect of the tolerance to submerged conditions.

*O. glaberrima* had already been known to be resistant to some biotic and abiotic stresses. The West Africa Rice Development Association (WARDA) which has conducted a project in interspecific hybridization between *O. sativa* and *O. glaberrima* since 1992, succeeded in the development of interspecific progenies with introduced strong resistance from *O. glaberrima*. The importance of *O. glaberrima* as a genetic resource, therefore, became a reality. In this study, several *O. glaberrima* lines were characterized in terms of physiological aspects of tolerance and also of morphological characteristics of avoidance of submergence, as mechanisms for the resistance to overflooding submergence.

**Materials and Methods**

Four *O. glaberrima* lines (TOG 5810, TOG 6283, CG 14 and CG 20) were used for the experiment with two *O. sativa* varieties (Norin 30 and IR 36) as checks. TOG 5810 and TOG 6283 were introduced from Nigeria and identified as submergence-resistant lines by the International Institute of Tropical Agriculture (IITA). CG 14 and CG 20 were introduced from Senegal and identified as drought-resistant and upland-adapted lines with high tillering and weed competitiveness. Norin 30 was identified as a submergence-resistant variety among the *O. sativa* subspecies of japonica type, and IR 36 was a standard indica type variety without any characterization of submergence resistance. The seeds were sown in a nursery box on 30 May, 1995 in the Experimental Field of the Faculty of Agriculture, University of Tokyo. On 18 July, a seedling was transplanted to a 1/5000 a Wagner pot which received 2 grams of compound fertilizer (N, 12%; P₂O₅, 15%; and K₂O, 15%). All the plants were grown under flooded conditions. Submergence treatment was applied to the potted plants on 31 August, by sinking them into the water stored in 2 m³ plastic tanks. All the lines and varieties were reaching the end of the stem elongation stage on 31 August. The position of the plants in the tank was changed every three days to eliminate the difference in the light environment in the tank.

Photosynthetic rate and chlorophyll content were determined for the leaves of the main stem in the same position (3 plants in each line) on 31 August and every several days after the submergence. The uppermost fully expanded leaves on 31 August were always used. The photosynthetic rate was determined with an oxygen electrode according to the method of Ishii et al. Chlorophyll content was determined according to the method of Schmid. Plant height was also measured for 3 plants used for the determination of the photosynthetic rate and chlorophyll content. Plant height under control conditions was measured for the plants grown under normal conditions. Water and air temperatures were monitored throughout the experiment, and no significant difference was observed in the water temperature between the tanks.

**Results**

Figure 1 shows the changes in the leaf chlorophyll content after the plants were exposed to submerged conditions. The initial content of leaf chlorophyll before the submergence treatment, was low in the *O. glaberrima* lines compared to the *O. sativa* varieties. The chlorophyll content showed a decreasing trend in all the lines and varieties after the initiation of the submergence treatment. However, the decreasing rate was different among them; the *O. glaberrima* lines showed a slow decrease, while the *O. sativa* varieties, particularly Norin 30 showed a rapid decrease. Figure 2 depicts the changes with the time of submergence in the photosynthetic oxygen evolution rate of a leaf slice (Ph). The trends of the changes of Ph were similar to those of the chlorophyll content in all the lines and varieties; the change of Ph was slow in the *O. glaberrima* lines throughout the experimental period, while the *O. sativa* varieties showed a rapid decrease. Figure 2 shows the changes with the time of submergence in the photosynthetic oxygen evolution rate of a leaf slice (Ph). The trends of the changes of Ph were similar to those of the chlorophyll content in all the lines and varieties; the change of Ph was slow in the *O. glaberrima* lines throughout the experimental period, while the *O. sativa* varieties showed a rapid decrease. The values of the chlorophyll content and Ph clearly indicated that the *O. glaberrima* lines were resistant, but that the *O. sativa* varieties, particularly Norin 30, a japonica variety, were not resistant to submerged conditions.

To analyze the avoidance mechanism under submerged conditions, plant height was examined after the initiation of the submergence treatment and the relative elongation rate to the initial height on 31 August was calculated (Fig. 3). *O. glaberrima* lines showed a much rapid elongation than *O. sativa* varieties under submerged
Fig. 1. Changes in chlorophyll content with the time of the submergence treatment. Vertical bars indicate standard deviation of three replications.
Fig. 2. Changes in the rate of photosynthetic oxygen evolution in a leaf slice with the time of the submergence treatment. Vertical bars indicate standard deviation of three replications.
Fig. 3. Changes in relative elongation rate to the initial plant height at 0 day with the time of the submergence treatment.
Vertical bars indicate standard deviation of three replications.
Closed circles, submergence; open circles, non-submergence (control).
The initial height of the submerged plants was as follows: TOG 5810, 114±7cm; TOG 6283, 96±5cm; CG 14, 88±7cm; CG 20, 113±6cm; Norin 30, 92±3cm; IR 36, 84±5cm.
The initial height of the control plants was as follows: TOG 5810, 118±5cm; TOG 6283, 94±4cm; CG 14, 96±4cm; CG 20, 122±6cm; Norin 30, 90±4cm; IR 36, 85±2cm.
conditions. Under normal growth conditions, the elongation was limited in both *O. glaberrima* lines and *O. sativa* varieties, and moreover, the difference in elongation was not significant between the lines and varieties. CG 14 showed a remarkably strong response of stem elongation soon after the submergence. The results of the measurement of plant height indicated that the *O. glaberrima* lines displayed a better avoidance mechanism to submergence than the *O. sativa* varieties.

**Discussion**

Two mechanisms determine the resistance of plants to environmental stresses: tolerance and avoidance. Tolerance is a physiological mechanism whereby the plants can maintain physiological activities even if they are exposed to stressed conditions, whereas avoidance is a morphological mechanism whereby the plants can avoid stressed conditions. In the present paper, the chlorophyll content and photosynthetic O<sub>2</sub> evolution rate were considered to be tolerance mechanisms, and stem elongation an avoidance mechanism.

The two lines of *O. glaberrima* used in the present study, TOG 5810 and TOG 6283 were identified by IITA as submergence resistant lines, and two other lines, CG 14 and CG 20 as drought resistant lines. In this experiment, however, no appreciable difference was found between the two groups of *O. glaberrima* in terms of the submergence resistance evaluated based on the changes in the chlorophyll content and photosynthetic O<sub>2</sub> evolution rate and also based on the changes in the plant height under submerged conditions. MORISHIMA *et al.*<sup>9</sup> reported that the *O. glaberrima* species cannot be classified into some subgroups, in the same way as *O. sativa*, which consists of several types. OKA<sup>10</sup> on the other hand, reported that there were two ecotypes in *O. glaberrima*: a deep water type and an upland type. In the present study we could not divide *O. glaberrima* into subgroups at least in terms of submergence resistance. Since the primary center of diversity of *O. glaberrima* is located in the swampy basin of the upper Niger River<sup>1</sup>, all the present lines of *O. glaberrima*, even the upland adapted lines, might have retained the ability of submergence resistance.

On the other hand, there was a significant difference in the mechanism of submergence resistance between the *O. glaberrima* lines and *O. sativa* varieties. It was considered that *O. glaberrima* is generally resistant to submerged conditions compared to *O. sativa*. Within *O. sativa*, indica rice, IR36 appeared to be more resistant than japonica rice, Norin 30, based on the changes in the chlorophyll content and photosynthetic rate. It will be impossible, however, to draw any conclusion for the difference between indica and japonica rice in terms of submergence resistance in this experiment, because only one variety was used as indica and japonica rice, respectively. However, Norin 30 was identified as one of the most resistant varieties of japonica rice to submergence<sup>17</sup>. Nevertheless, IR36 and four *O. glaberrima* lines showed a stronger resistance to submergence than Norin 30, suggesting that the japonica type is not resistant to submerged conditions.

In some cases, the avoidance mechanism, like stem elongation, and the tolerance mechanism, like maintenance of physiological activities, cannot coexist within one species. In our preliminary study, FR13A, an indica variety developed at IRRI, showed a very strong physiological tolerance to submerged conditions in terms of photosynthetic maintenance, but the ability of stem elongation was much lower than that of IR 36. However, the *O. glaberrima* lines displayed a tolerance mechanism to submergence along with the avoidance mechanism. These characteristics of *O. glaberrima* will be important as adaptation mechanisms to medium deep or deep water conditions. Since CG 14 and CG 20 are listed among the *O. glaberrima* lines used for the interspecific hybridization program with *O. sativa* at WARDA<sup>5,6,14</sup>, they could become suitable breeding materials for interspecific rice varieties adopted to deep water conditions.

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**References**


