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Complete submergence escape with shoot elongation ability by underwater photosynthesis in African rice, *Oryza glaberrima* Steud.

Jun-Ichi Sakagami*, Yukiko Joho, Chiharu Sone

Crop, Livestock & Environment Division, Japan International Research Center for Agricultural Sciences, 1-1 Ohwashi, Tsukuba, Ibaraki 305-8686, Japan

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ABSTRACT

Flooding imposes severe selection pressure on plants, principally because excess water in their surroundings deprives the plants certain basic resources such as oxygen, carbon dioxide, and light for photosynthesis. In recent years, reports of damage caused by flooding to rice plants have increased concomitantly with the expansion of rainfed lowland rice cultivation throughout the world. Strong submergence-induced elongation, a common escape mechanism, helps submerged individuals regain and retain contact with the aerobic environment. This study analyzed physiological mechanisms of escape from complete submergence by evaluating photosynthesis, photochemical reaction, and plant behavior during and after submergence in *Oryza glaberrima* Steud. Partially submerged plants were unaffected by excess water because their photosynthetic rate was maintained during and after submergence. Escape mechanisms, when under complete submergence, restrain shoot elongation per shoot dry weight per day during submergence (shoot elongation index). Our results demonstrate that the leaf area and shoot biomass of the submerged plants during submergence affects their post-submergence photosynthetic rate and the PSII maximum efficiency to some degree. Under deeply prolonged submergence, *O. glaberrima* genotypes were characterized by faster shoot elongation, anaerobic tillering, larger leaf area extension, higher photosynthetic rate, and maintenance of PSII maximum efficiency compared with *Oryza sativa* genotypes without an escape mechanism. *O. glaberrima* employs a submergence escape strategy that effectively uses stored carbohydrates for shoot elongation and leaf extension in a severely photosynthesis-limited environment under complete submergence.

1. Introduction

In Africa, according to the water regime, wetlands for rice cultivation are classified into irrigated lowlands, rainfed lowlands, deepwater, and mangrove swamps. Since 1988, reports of damage to rice plants in wetlands due to flooding have been increasing along with the expansion of rainfed lowland rice cultivation (Hallegatta et al., 2010). Therefore, damage to rice plants by submergence differs depending on the distinctive water environment, as determined by water depth, duration of submergence, temperature, turbidity, rate of nitrogen fertilizer application, and light intensity (Palada and Vergara, 1972). Rice is the only major crop that is adapted to aquatic environments because of its aerenchyma tissues, which facilitate gas diffusion, and leaf gas film, which enables internal aeration between submerged tissues and water (Colmer and Pedersen, 2008; Raskin and Kende, 1983). However, prolonged and complete submergence affects rice growth and yield because of anaerobic fermentation. In general, leaf photosynthesis decreases under complete submergence because of CO_2 depletion and low irradiation, resulting in decreased supply of carbohydrates following degradation of photosynthesizing tissues. An important adverse effect of shoot elongation, which is the response frequently observed in rice plants under complete submergence, is an increase in carbohydrate consumption for cell division, cell elongation, and leaf elongation maintenance (Ito et al., 1999; Setter and Laureles, 1996; Voesenek et al., 2006). Submergence escape with faster shoot elongation enables rice to resume functioning when aerobic conditions recur (Sakagami et al., 2009). However, little is known about the physiological mechanisms of submergence escape, which is driven by shoot elongation ability with CO_2 exchange under water in prolonged complete submergence. This escape strategy has been characterized by rapid elongation of internodes in response to complete submergence (Colmer and Voesenek, 2009). Sakagami et al. (2009) recently indicated that leaf sheath and blade development during shoot elongation in the vegetative stage could be considered as a submergence escape mechanism in cases of deepwater flooding. *Oryza glaberrima*, a monocarpic annual species of rice derived from *Oryza barthii* and originating in Africa (Sakagami et al., 1999), is grown traditionally. It is highly adapted to deepwater flooding in the wetlands of West

* Corresponding author. Tel.: +81 29 838 6368; fax: +81 29 838 6355.
E-mail address: sakajun@affrc.go.jp (J.-I. Sakagami).

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Africa. Deepwater flooding-adapted rice can survive flooding stress through rapid shoot elongation and greater extension of submerged leaves (Sakagami, 2012). The potential adaptability of *O. glaberrima* is important for genetic improvement, but its cultivated area has diminished rapidly because of low yield resulting from grain shattering. *O. glaberrima* genotypes are generally susceptible to flash floods with short-term complete submergence because lodging, which occurs readily after desubmergence, triggers increased plant mortality (Joho et al., 2008). Deepwater flooding-adapted rice can maintain aerobic metabolism during submergence via development of its canopy above the water surface because of elongation of its long leaves (Sakagami and Kawano, 2011). 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 triggering 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 as a result of the fact that gas diffusion is 10^4-fold slower in liquid (in this case water) than in air (Armstrong, 1979). Hattori et al. (2009) identified *SNORKEL1* and *SNORKEL2* as deepwater flooding-response genes for elongation for long-term submergence escape. However, enhancement of shoot elongation by small seedlings during submergence in water that is too deep to permit re-emergence presents a futile escape strategy (Kawano et al., 2009). Vigorous upward leaf elongation during prolonged submergence is therefore critical for ensuring shoot emergence from deepwater flooding (Sakagami et al., 2009). However, "anaerobic tillering capacity," which represses dormant tiller buds under water, has not been discussed well as an escape strategy in rice. In general, submergence escape strategies of rice are characterized by shoot elongation with rapid leaf extension in low oxygen escape syndrome or by rapid internodal or stem elongation, which enables contact with air. Effectiveness of the latter depends on water depth and flooding duration. In addition, in rice plants, distribution of the photoassimilated product or/and photosynthetic capacity is altered by deepwater flooding (Hirano et al., 1995). Irrespective of the outcome, rapid shoot elongation involves the risk of depleting conserved plant carbohydrates during complete submergence (Sakagami and Kawano, 2011). This study analyzes in detail the submergence escape mechanism that utilizes effective shoot elongation to accelerate photosynthetic capacity in the genotype of *O. glaberrima* Steud., which is adapted to flood-prone areas in Africa. An understanding of the submergence escape mechanisms used by rice plants to survive deepwater flooding might contribute to future biotechnological improvements of rice varieties grown in flood-prone areas.

2. Materials and methods

2.1. Experiment 1: field experiments

The experiment was conducted with 66 cultivars: 36 cultivars of *Oryza sativa* L., including 6 submergence-tolerant genotypes donated by the International Rice Research Institute (IRRI) and 30 of *O. glaberrima* Steud. All cultivars were sown directly in a nursery with lowland soil of pH 4.2. Fifteen-day-old seedlings were transplanted to an irrigated experimental field at the Foulaya Agricultural Research Center (FARC) in the Republic of Guinea (10°0′N, 12°9′W, elevation 330 m) during rainy season in 2005 and 2006. Plants were thinned to three seedlings per hill 10 d after transplanting. Plants were grown with three replications per cultivar in the field. During the experiment in 2005, the daily average for solar radiation with photosynthetic photon flux density, air temperature, and relative humidity were approximately 1267 μmol m^{-2} s^{-1}, 26.3 °C, and 78.2%, respectively. Whereas, during the experiment in 2006, the daily average for solar radiation with photosynthetic photon flux density, air temperature, and relative humidity were approximately 1150 μmol m^{-2} s^{-1}, 27.4 °C, and 70.5%, respectively. Twenty days after transplanting, all plants were completely submerged under a water depth of 40 cm for 32 d. The average pH and concentration of dissolved oxygen in flood water were 4.7 and 6.1 mg L^{-1}, respectively, in 2005 and 4.9 and 6.9 mg L^{-1}, respectively, in 2006. Measurements were taken before and after submergence for the survival rate in 2005 and shoot length, tiller number, and shoot dry weight in 2006. Plant survival was assessed on the basis of their appearance.

2.2. Experiment 2: pot experiments in the open air

2.2.1. Plant materials

This study compared different genotypes of shoot elongation (IR62293-2B-18-2-2-1-3-2-3: IR62293) and submergence tolerance (IR67520-B-14-1-3-2-2: IR67520) containing the *Sub1* gene in *O. sativa* and CG14 in *O. glaberrima* during dry season in 2006. These genotypes were chosen from experiment 1. The *O. glaberrima* genotype was a local cultivar from Senegal. In this study, submergence tolerance is defined as the ability of rice plants to survive without shoot elongation for 10–14 d under complete submergence and to resume growth when flood waters subside (Setter et al., 1995).

2.2.2. Growth conditions

Two pre-germinated seeds were sown in 2-L plastic pots filled with dried paddy soil characterized as sandy (pH, 4.2 before sowing). Seventeen-day-old seedlings were submerged in a 5130-L outdoor concrete tank for 40 d under a water depth of 40 cm as a partial submergence plot and with 60 cm as a complete submergence plot, with 15 d of no submergence for post-submergence recovery, at FARC. Seedlings of the same rice genotypes were placed in the concrete tank without submergence as controls. The experiment used a randomized complete block design with five replications per cultivar. Furthermore, flood waters were kept almost clear during submergence and all plants were submerged completely and partially at the beginning of submergence treatments. The average water temperature during the day at a depth of 30 cm and at surface were 25.3 °C and 26.1 °C, respectively, and the mean photosynthetic photon flux density at 50 cm above the water surface at 12:00 was 929 μmol m^{-2} s^{-1}. The average pH and concentration of dissolved oxygen in flood water in the tank were 4.2 and 8.9 mg L^{-1}, respectively.

2.2.3. Measurements

Three plants of each genotype were selected from the replicated pots for taking measurements of shoot length and leaf area measurements using an automated area meter (AAM-9; Hayashi-Denko Co. Ltd., Japan). Measurements were taken 1 d before submergence and 10 d, 25 d, 40 d, and 55 d after submergence. Leaf area was measured using part of a leaf blade taken from a whole plant. Stomatal conductance of a fully developed upper leaf from above the water surface was observed in the morning (9:00–10:30) 0 d, 12 d, 19 d, 33 d, 40 d, and 55 d after submergence using a porometer (AP4; Delta-T Devices Ltd., UK). Statistical analysis was performed using Tukey–Kramer test for multiple comparisons.

2.3. Experiment 3: pot experiments in the growth chamber

2.3.1. Plant materials

This experiment was conducted at the Japan International Research Center for Agricultural Sciences in Tsukuba, Japan using shoot elongation genotype (IR71700-247-1-1-2: IR71700),