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Submergence tolerance in relation to variable floodwater conditions in rice

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ABSTRACT

Flash floods adversely affect rice productivity in vast areas of rainfed lowlands in South and Southeast Asia and tropical Africa. Tolerant landraces that withstand submergence for 1–2 weeks were identified; however, incorporation of tolerance into modern high-yielding varieties through conventional breeding methods has been slow because of the complexity of both the tolerance phenotype and floodwater conditions, and the ensuing discrepancies encountered upon phenotyping in different environments. Designing an effective phenotyping strategy requires a thorough understanding of the specific floodwater characteristics that most likely affect survival during flooding. We investigated the implications of floodwater temperature and light penetration, caused by artificial shading, seasonal variation, or water turbidity, for seedling survival after submergence. Three field experiments were conducted using rice genotypes contrasting in their tolerance of submergence: FR13A and Kusuma (tolerant); Gangasiuli (intermediate); Sabita, CRK-2-6 and Raghukunwar (elongating/avoiding types); and IR42 (sensitive). We tested the hypotheses that warmer floodwater decreases plant survival and that turbid water augment plant mortality by causing effects similar to those caused by shading, by reducing light penetration. Plants survive better when water is cooler, and survival decreased at about 8% per unit increase in water temperature above 26 °C. Lower intensity of light and warmer temperatures seem to reduce biomass and increase mortality under flooding. An increase in the concentrations of O_2 and CO_2 and a decrease in water pH did not improve survival in clear unshaded water. Turbid floodwater was more damaging to rice as plant mortality increased as the percentage of silt increased, and the effects of water turbidity cannot be explained by the reduction in light penetration alone. Even the most tolerant rice cultivar, FR13A, experienced higher mortality when flooded with turbid floodwater. Correlation studies revealed that cultivars with the capacity to maintain higher biomass, higher chlorophyll, and non-structural carbohydrate concentrations after submergence had higher survival. These findings help to understand the variation observed in submergence tolerance when screening is done under different environments. The study could have implications for designing proper screening strategies and assessing the damage submergence causes across different rice-growing regions.

1. Introduction

Flooding affects vast rainfed lowland rice areas in Asia during the monsoon season. In deepwater and floating-rice areas, water stagnates for a longer duration, commonly more than a month, and genotypes adapt to these conditions through faster shoot elongation to avoid complete inundation (Setter and Laureles, 1996). Transient submergence for periods of up to 2 weeks can also occur in some areas, at any time and mostly more than once during the growing season because of flash floods caused by either heavy rains or outflow of nearby rivers. This type of flooding affects more than 22 million ha of rainfed lowlands in South and Southeast Asia, of which over 6 million ha are in India (Khush, 1984; Sarkar et al., 2006). Modern high-yielding rice varieties are always sensitive to complete submergence; however, numerous tolerant landraces were identified before (Mackill et al., 1993). Physiological mechanisms associated with tolerance of flash-flooding during germination (Ismail et al., 2009) as well as during the vegetative stage were studied extensively (Setter et al., 1997; Ram et al., 2002; Jackson and Ram, 2003; Sarkar et al., 2006).

Submergence tolerance in rice is physiologically complex but seems to be genetically simple (Xu and Mackill, 1996; Xu et al., 2006). The Indian cultivar FR13A is the most widely studied and used source of submergence tolerance in rice breeding, and a major QTL, designated *SUB1*, was identified that controls most of the submergence tolerance of this genotype (Xu and Mackill, 1996). FR13A

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also has additional QTLs that contribute to its tolerance (Nandi et al., 1997; Toojinda et al., 2003). *SUB1* was subsequently fine-mapped and cloned, and three genes encoding putative ethylene responsive factors (ERF), *SUB1A*, *SUB1B*, and *SUB1C*, were identified, with *SUB1A* recognized as the primary determinant of submergence tolerance (Xu et al., 2006). Cloning of *SUB1A* provided opportunities to gain more insight into the molecular mechanisms involved and to unravel the pathways underlying the submergence tolerance conferred by this gene (Fukao et al., 2006; Fukao and Bailey-Serres, 2008). Moreover, precise gene-based markers were designed for *SUB1* and used for its successful introgression into popular high-yielding rice varieties (Neeraja et al., 2007; Septiningsih et al., 2009). Subsequent testing of introgression lines in the field showed no apparent effects on agronomic performance, grain yield, or quality in the absence of submergence (Sarkar et al., 2006; Neeraja et al., 2007), but with substantial enhancement in survival and yield (by 2–3-fold) after submergence for 12–17 d (Authors' unpublished data).

Damage to plants caused by submergence could have several causes linked to floodwater conditions, particularly the interference in normal gas exchange and light interception. The adverse effects of flooding on rice vary by genotype, and of particular importance are the carbohydrate status of the plant before and after submergence, the developmental stage at which flooding occurs, duration and depth, and the level of turbidity and turbulence of floodwater (Setter et al., 1995; Jackson and Ram, 2003; Das et al., 2005; van Eck et al., 2005; Colmer and Pedersen, 2008). Aspects of the floodwater environment are commonly variable at different locations, and even over short distances (Setter et al., 1988). Since gas diffusion in water is 10,000 times slower than in air (Armstrong, 1979), restricted diffusion of the most important gases, oxygen and carbon dioxide, is considered the most limiting environmental factor under flooded conditions. The plant hormone ethylene also accumulates in plants during submergence because its diffusive escape is inhibited while its synthesis is promoted by flooding (Jackson et al., 1987). Enhanced ethylene concentration in submerged plants could promote: (i) under-water elongation during submergence as observed in rice (Jackson, 2008) and in *Rumex palustris* L. (Voesenek et al., 1993) and (ii) chlorophyll degradation and leaf senescence (Jackson et al., 1987; Ella et al., 2003) that may reduce photosynthetic carbon fixation during and after submergence. Both elongation growth and a reduction in concurrent carbon fixation during submergence can result in a depletion of carbohydrate reserves with a consequent increase in plant mortality. Elongation during submergence is undesirable because energy required for elongation competes with maintenance processes, and its adverse effects on survival after complete submergence were reported before (Jackson et al., 1987; Setter and Laureles, 1996; Singh et al., 2001; Das et al., 2005). Processes and conditions that enhance plant elongation under complete submergence could therefore counteract plant survival.

Another important factor in submergence is poor light transmission through floodwater, particularly in the presence of thick algal growth or higher water turbidity (Setter et al., 1995; Whitton et al., 1988). Light reaching the leaves of submerged plants is attenuated by water, dissolved organic matter, silt, and/or phytoplankton suspended in the floodwater. When floodwater is turbid, only a scanty amount of solar radiation reaches the canopy level and thus limits the capacity of plants for under-water photosynthetic carbon fixation (Setter et al., 1995). Sediment load in floodwater, cloudiness during the monsoon season, and water depth also affect light transmission and the extent of shading of submerged plants. Increased shading during submergence causes greater injury and promotes plant mortality in rice (Adkins et al., 1990; Jackson and Ram, 2003). The under-water light regime is also a major controlling factor of CO_2 and O_2 concentrations in floodwater that determine the extent of photosynthesis and metabolism of submerged plants (Ramakrishnayya et al., 1999; Panda et al., 2006, 2008). The importance of photosynthesis during submergence in rice was supported by the results of experiments in which CO_2 concentration was manipulated by altering floodwater pH. Low water pH or enhanced concentration of CO_2 is known to enhance photosynthesis under submerged conditions and improve survival (Setter et al., 1989; Ramakrishnayya et al., 1999). Low water temperature may decrease respiratory costs, since the rates of both anaerobic and aerobic metabolism decreased at lower ambient temperature (van Eck et al., 2005). An indirect effect of water temperature is the higher solubility of oxygen in cold water compared with warm water, which could help avoid damage due to tissue anoxia.

The role of variable floodwater characteristics on survival of rice after the floodwater recedes has been described before, but mostly based on indirect evidence derived from inferences of studies on floodwater conditions in naturally flooded fields (Setter et al., 1995). Systematic analysis of the effects of these individual factors and their interactions is essential to help interpret the commonly encountered variation in responses to flooding at different geographical locations and in different seasons. In this study, we attempt to investigate and compare the effects of variation in water temperature caused by shading or seasonal variation, the effects of different levels of light intensities and water turbidity, and the consequent changes in other parameters such as concentrations of CO_2, O_2, and floodwater pH, on the survival of rice genotypes contrasting in their tolerance of submergence. We hypothesize that (1) warmer water increases seedling mortality, possibly through increased carbohydrate depletion during submergence and that (2) turbid water will enhance plant mortality by effects similar to those caused by natural shading, the common consequence of cloudiness during the wet season. This could be caused by reduction in light penetration, the subsequent chlorophyll degradation and reduced under-water photosynthesis. Rice breeders in some countries have tried to simulate flooding with turbid water through artificial shading, but with inconsistent results, particularly over seasons. The study could help develop effective phenotyping strategies that can simulate actual field conditions at target sites.

2. Materials and methods

2.1. Plant material and growth conditions

Three experiments were conducted at the Central Rice Research Institute (CRRI), Orissa, India (20.5°N, 86°E, and 23.5 meters above mean sea level), to study the effects of light intensity and water temperature and turbidity on the survival of contrasting rice (*Oryza sativa* L.) genotypes after complete submergence. In all three experiments, rice genotypes were sown directly in earthen pots each containing 2 kg of farm soil and farmyard manure in a 3:1 ratio. Each pot was supplemented with 80 mg of urea, 192 mg of single superphosphate (P_2O_5), and 70 mg of murate of potash (K_2O). Ten seeds were sown per pot and later thinned to five seedlings 10 d after germination. Twenty-one-day-old seedlings were then completely submerged in concrete tanks at a depth of 110 cm of water for 10 d (Das et al., 2005). All experiments were conducted in concrete tanks under natural field conditions.

Seven rice genotypes were evaluated in three different experiments: FR13A (tolerant) and IR42 (sensitive) were used in all experiments, as both genotypes were frequently used in the past as checks during screening and also in numerous physiological studies (e.g. Ella et al., 2003; Das et al., 2005). Sabita, was used only in Experiment I, and CRK-2-6 was used in Experiments I and III. CRK-2-9 is a high-yielding variety with erect leaves. Kusuma (tolerant), Gangasiuli (intermediate), and Raghukunwar were used in Experiment III. Sabita, CRK-2-6 and Raghukunwar are elongating