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How Rice (*Oryza sativa* L.), a Semi-Aquatic Plant Adapt to Natural Flood or Submerged Condition? A Physiological Perspective

(Bagaimana Padi (*Oryza sativa* L.), Suatu Tumbuhan Akuatik Menyesuaikan Diri dalam Keadaan Banjir Semula Jadi atau Tenggelam? Suatu Perspektif Fisiologi)

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ABSTRACT

The deficiency of oxygen in water during submergence is one of the frequently perceived environmental factors that limits or hampers production of the rice cultivation. Rice plants comprise of elongated submerged tissues that help to bear with the rise of water level in natural location. This characteristic helps the plant to deal with flooding stress. The mechanism on flooding tolerance and adaptation mostly includes the physiological changes, one of which is the shortened growth of elongation towards keeping the carbohydrates and energy for production of the antioxidant regulations in rice plants. Furthermore, molecular studies and gene cloning might help suggest a better understanding of means and adaptations built-up by rice plants in order to stay alive and to remain active during flooding stress, might help to focus on some novel approaches to the up gradation as well as improvement on the natural cultivation of rice plants.

Keywords: Adaptation; anoxia; biochemical change; flooding; Oryza sativa*; submergence*

ABSTRAK

Kekurangan oksigen dalam air semasa penenggelaman adalah salah satu faktor alam sekitar yang sering dilihat menghadkan atau menghalang pengeluaran penanaman padi. Tanaman padi terdiri daripada tisu tenggelam memanjang yang membantu mengatasi kenaikan paras air di lokasi semula jadi. Ciri ini membantu tumbuhan untuk menangani tekanan banjir. Mekanisme banjir dan penyesuaian selalunya melibatkan perubahan fisiologi, satu daripadanya ialah pemendekan pertumbuhan pemanjangan ke arah menjaga karbohidrat dan tenaga untuk pengeluaran antioksidan dalam tanaman padi. Selanjutnya, kajian molekul dan pengklonan gen boleh membantu mencadangkan cara yang lebih difahami dan penyesuaian binaan oleh tanaman padi untuk terus hidup dan kekal aktif semasa tekanan banjir, dapat membantu untuk memberi tumpuan kepada beberapa pendekatan novel untuk meningkatkan pemeringkatan serta penambah baikan penanaman tanaman padi secara semula jadi.

Kata kunci: Anoksia; banjir; Oryza sativa*; penyesuaian; perubahan biokimia; tenggelam*

INTRODUCTION

Rice is one of the most important economic crops of Assam and other hilly terrains of India. Rice, though a semi - aquatic plant, is adapted to survive flooding or submergence for a certain period of time. A total of about 22 million hectares of rice-growing area in India is unfavourably affected by submergence or flash flooding, half of which is in Eastern India (Roy 1993). In India, generally, rice suffers from submergence during June to September every year. Quite lots of studies have suggested that rice plant responds to different stresses, including that of flooding or submergence at biochemical, molecular and cellular as well as physiological levels. Usually, rice has two main cultivars, the *Indica rice* and the *Japonica rice*, of which the former is regularly cultivated in India. The appearance of variety of genes encouraged by these stresses and their role in tolerance, regulation of gene expression and signal transductions in stress response, has also been confirmed by many authors (Dolferus et al. 2003; Lee et al. 2007; Subbaiah & Sachs 2003). Rice genotypes, FR13A tolerant of complete submergence at the vegetative stage, has showed a good yield gain following submergence or flooding for more than a few weeks up to 10 to 20 days (Mackill et al. 2012). As submergence or flash flooding may boost up generation of reactive oxygen species (ROS) within the cell, particularly within the chloroplast of submerged stress plants, it leads to lipid peroxidation, protein degradation, enzyme inactivation; and almost every constituent of the cell exposes to cell death (Bansal & Srivastava 2012; Blokhina et al. 2003; Upadhyay et al. 2010). This review depicted some physiological characteristics of adaptations and mechanisms completed by rice plants in order to struggle or to deal with the flooding during rice cultivation.

Avoidance Mechanism

Rice plants adapted through external and internal gas spaces and the elongated growth during flooding helped the plant to maintain contact to the air. Amongst the deep water rice diversities, floating rice has the maximum elongation capacities (Vergara et al. 1976). Rice plants survive or, for that matter, the survival of rice plants depends on their ability to face the rise of water during their durational increase in submergence, from a few hours to week. Needless to say, this application also enhances the production of crops, since the juvenile seedlings as well as matured plants have an equal ability to contribute to the growth of fast elongation when partially flooded in water. Generally, growth takes place at younger internodes, having active intercalary meristem which is located at the base of the node. Thereby, it releases cells into elongation zone above it (Kende et al. 1998). However, the formation of some new roots at the nodes of submerged rice plants helps to keep distance over which oxygen deficiency has to be transported. Likewise, the adventitious root helps the plant parts with minerals and water supply. The emerged root initials occur only when the plants get under water. Submergence stress increases the membrane damage, as was evident from the increased value of electrical conductivity and lipid peroxidation. Similar report was observed in sorghum and rice plants (Hsu et al. 2000; Upadhyay et al. 2009).

On the other hand, ethylene acts as hormonal signal, together with the gibberellins and abscisic acid, helping in inducing the growth of the plants. Induction of cell elongation and cell division activity as well has been studied (Kutschera & Kende 1988; Metraux & Kende 1984). However, in some rice plants, the growth of internodes, including the adventitious roots, is sustained by a high cell production rate. In roots, mostly adventitious, it acts as a growth inducer, while auxin, gibberelin, cytokinin are ineffective, as reported by Lorbiecke and Sauter (1999). However, as shown in Figure 1, the growth of stem, ethylene acts as an intermediary signal that induces changes in the abundance of absicic acid (ABA) and gibberellins (GA). ABA decreases whereas GA increases under flooding stress (Hoffmann- Benning & Kende 1992). As reported, ethylene induces the growth of plants under submergence as a whole, stimulating shoot elongation in both aquatic and semi-aquatic plants. Plant continuously produces ethylene in small amounts, but submergence leads to accumulation of physical entrapment of water by which ethylene enhances shoot elongation in rice plants. This mechanism helps increase the chance of survival of plants under submergence or flooding. It also induces the formation of aerenchyma. The response of ethylene in rice and other similar plants in aquatic conditions is opposite to that of the terrestrial plants where ethylene usually inhibits growth and induces senescence (Jackson 1997). The biosynthesis of ethylene on plants under flooding is associated with the induction of ACC Synthase and ACC Oxidase genes (Zhou et al. 2001). However, a comparable

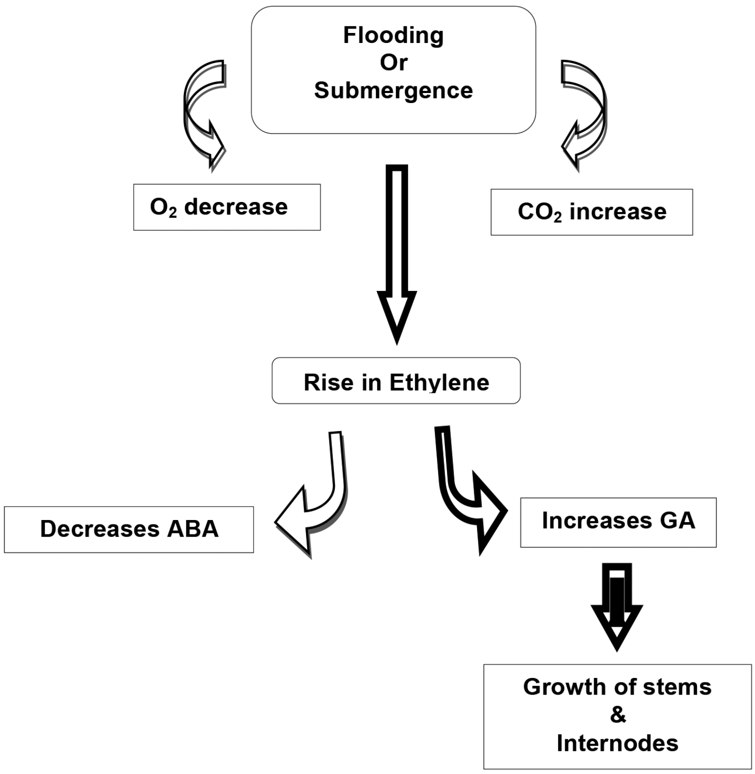

FIGURE 1. Regulation of Hormones induced under flooding stress in rice plants. This diagram is based on Hoffmann-Benning and Kende (1992) and has been updated with more recent research findings

hormonal interaction regulates an enhanced growth upon complete submergence or flooding, which is frequently visible in both lowland and deepwater rice seedlings (Vander Straeten et al. 2011).

Tolerance Mechanism

Flooding tolerance is a metabolic adaptation in response to anaerobiosis that enables cells to maintain their integrity and the plant to survive without major damage. Rice plants adaptation to submergence involves in combination of one or more factors such as morphological, anatomical and metabolic in nature. Formation of aerenchyma reduces internal impedance towards transportation of oxygen and other gases such as CO_2 and ethylene between roots and shoots. Such transport promotes radial oxygen loss roots, leading to oxidative detoxification of the rhizosphere. Root facilitates diffusion of gases in or out of the plants. The shoot portion above water plays a critical role in transportation of oxygen to the submerged portions (Ram et al. 2002). During flooding, aerenchyma formation occurs in internodes of rice plants by ethylene promoting formation of $O_2^{\cdot-}$, H_2O_2; whereas in lowland rice, this occurs upon flooding in leaf sheaths of rice cultivars (Parlanti et al. 2011; Steffens et al. 2012). Thus ROS can be regarded as an inner regulator of rice plant adaptation towards flash flooding or submergence. According to Mcmanmon and Crawford (1971) theory, flood tolerance in plants depends on decrease in ethanol production, due to low ADH activity that helps to reduce the toxic effects of ethanol. During flooding, the ATP requires keeping anaerobic tissue alive, and it is generated by the fermentation process. The role of carbohydrate is probably to act for survival of the plants. Old seedlings tend to have a large carbohydrate reserves and therefore, these enhances the good survival of plants during submergence (Singh et al. 2001). The alcoholic fermentation pathway is the main source of energy production. ADH and PDC are the enzymes mainly responsible for flood tolerance. In rice plants, PDC and ADH have important role to play, since PDC is the enzyme channelling carbon followed by the ADH that limits the rate of ethanol formation. Overall, it appears to be a significant step towards avoiding the accumulation of acetaldehyde (Grover et al. 1995).

Rice plants tolerate flooding or they endure complete submergence for a period of about 5 days, even though variation exists among different varieties or cultivars. Comparison of the various flood-tolerant and intolerant rice varieties in the field experiments indicated that the seedlings of the tolerant species contain 20-30% more starch than those of the intolerant varieties. These starch reserves were rapidly used up on the submergence (Sarkar et al. 1996). Ethanolic fermentation was identified to be the main route of glucose metabolism in aerobic rice seedlings (Menegus et al. 1991). In rice, on the other hand, a modified pattern of polypeptides was observed during anoxic growth. Most of the newly synthesized proteins represent the enzyme of sucrose metabolism, glycolysis and fermentation, stressing the importance of carbohydrate metabolism for the survival of the plant. The ability to induce α - amylase activity under anoxic conditions has been implicated fewer than one of the important adaptations of rice to growth under water. Haq and Hodges (1999) identified two genes which were members of a gene family from rice that induced early after onset of anoxia. Rice plants grow well in flooded or submerged soil due to the efficiency of ventilation, acquired by the formation of air-spaces with the tissue to improve the exchange of gases between the submerged plant parts and the atmosphere (Jackson & Armstrong 1999).

Another morphological adaptation to flooding, controlled by ethylene, is the formation of adventitious roots formed at nodes of the stem (Lorbiecke & Sauter 1999). These roots help assimilation of water and minerals by the young tissues in addition to assisting the anchorage of the plant on the soil once the water level recedes. Rapid stem elongation induced by submergence is of utmost importance for the survival of deepwater rice, when the plants remain submerged for several months (Kende et al. 1998). Slow growth during flooding is suggested as a way to sustain high carbohydrate reserve and to prolong the energy supply for maintaining the process in all submerged rice plants. In fact, the submergence-tolerant lowland varieties FR13A have higher total soluble carbohydrate content than that of the susceptible one, *viz Mahsuri,* and it prevents lower starch depletion rates during submergence treatment (Singh et al. 2001). Rice is more tolerant to ethanol than other cereals, and can easily germinate by 1.6% ethanol in normal cases (Alpi et al. 1985).

Conclusion and Recommendation

Rice is an important crop in tropical and subtropical regions of the world. Environmental stresses-mostly abiotic in nature-submergence stress or flash flooding, are the major factors responsible for limiting the productivity in rice cultivation. Deepwater rice is the only crop that can be cultivated in some regions in south and south-east Asia. For this reason, an improvement of high yielding lowland rice, displaying an equally high tolerance towards a temporary but submergence is of major agronomic importance. The metabolic adaptations that form the basis of several related genes were, however, unspecific for flood-tolerant rice cultivars, which seemed to make the difference. Therefore, it is felt that these novel techniques would help us to unravel the mechanism that initiates the response and development of the tolerant genotypes, which are the key areas where research to increase crop productivity and to standardise the flood - prone farmers are crucial.

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