

Snorkeling Strategy

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Flooding is an important strategy for weed control in paddy rice fields. However, terrestrial weeds had evolved mechanisms of tolerance to flooding, resulting in new 'snorkelling' ecotypes. Several weeds, mainly weedy rice, have evolved submersion tolerance mechanisms, which could be called snorkelling strategy, which are strategies that guarantee its survival and perpetuation in flooded environments. Current advances in biotechnology present the possibility of using molecular tools to understand flooding tolerance and manipulate DNA and RNA for the development of modern snorkelling weed control methods

[rice](#)[Echinochloa](#)[weedy rice](#)[SUB1](#)[SK1](#)[Flooding tolerance](#)[Hypoxia](#)[Rice Diversity](#)

1. Introduction

Flooding is the most efficient cultural method for controlling flood-sensitive weeds soon after rice sowing. Water management characterizes the different rice establishment systems, such as dry-seeding, water-seeding or transplanting ^[1]. These systems were developed to provide water for the rice crop and to control weeds. Therefore, although rarely acknowledged, water is a natural herbicide used in flooded crop agriculture. However, since rice domestication, weeds had co-evolved with rice, and flood-tolerant weeds became one of the main problems in rice production. Transplanting and water-seeding systems are more efficient for weed control than dry-seeding, especially for weedy rice, which is one of the most important constraints of rice production worldwide. However, weedy rice is also adapting to flooding ^{[2][3]}, perhaps more than the other rice weeds, and this presents a serious challenge for the utilization of water management strategies to establish rice. The changes in metabolism and morphological growth processes of weedy rice that escape flooding suggests evolution for tolerance to this abiotic stress ^[4].

2. Mechanisms of Tolerance to Flooding in Rice and Weedy Species

2.1. Tolerance to Flooding during Germination

Seed germination is driven by a complex regulatory system. The energy demand during germination is high; numerous exogenous and endogenous factors affect this process, mainly associated with oxygen availability. Germinating seeds in normal oxygen conditions ($O_2 \geq 21\%$) derive energy via the electron transport chain and

oxidative phosphorylation using O_2 as final acceptor of electrons. Under anaerobic condition, the electron transport chain and oxidative phosphorylation are inhibited by lack of O_2 ; the plant then turns on glycolysis to generate energy. Glycolysis is an inefficient process of generating ATP; thus, anoxia prevents germination of most species. To obtain sufficient energy for normal physiological function in flooded conditions, more carbohydrates are mobilized toward glycolysis; anaerobic respiration, or fermentation, is activated. The evolved ability to maintain metabolic processes under low O_2 allows the germination and emergence of some species in flooded conditions. Examples of these species are *Echinochloa spp.*, *Arundinella anomala*, *Sagittaria montevidensis*, *S. trifolia*, and weedy rice, which are major weeds of rice [2][5][6].

The evolved flood-tolerant ecotype of *C. rotundus* stores more non-structural carbohydrates, which serve as a substrate for anaerobic metabolism, compared to the normal flood-sensitive ecotype [7]. Tolerant ecotypes have larger tubers with about twice more non-structural carbohydrates than susceptible plants [7]. However, just producing more carbohydrates does not guarantee an increase in anaerobic metabolism. The plant also has to be able to convert these carbohydrates into glucose, which is the form of sugar that is transported and used in glycolysis. Therefore, adequacy in the complex network of metabolic processes is required for the evolution of tolerance to submersion. Low oxygen triggers the formation of ethylene, which induces the expression of genes related to carbohydrate conversion and maintenance of anaerobic respiration. Rice seeds that germinate well under low oxygen supply have higher expression of *RAmy3D* than in rice varieties intolerant to hypoxia [8]. Overexpression of *RAmy3D* gene in the coleoptile and endosperm of transgenic rice genotypes increased the germination capacity under anoxic conditions [9]. *RAmy3D* codes for alpha-amylase, which is involved in the catabolism of carbohydrates during germination. Concomitantly, the sucrose synthase (*SUS3*) gene promotes the production of soluble sugars when oxygen is deficient [10]; thus, providing the substrate for ATP production under oxygen-deficient environments (Figure 1).

The ATP supply for metabolism under anoxic conditions is enabled by the maintenance of the glycolytic pathway that promotes the regeneration of NAD^+ . This process is enabled by the consumption of pyruvate by fermentation, avoiding the accumulation of this by-product of glycolysis and decrease of the glycolytic flux due to NAD^+ limitation [11]. Lactic acid fermentation starts with the production of lactate (facilitated by lactate dehydrogenase, LDH), which acidifies the cytoplasm and activates alcoholic fermentation by the action of pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH), and producing ethanol [12]. These reactions are maintained through the oxidation of NADH in the mitochondrial matrix. In this process, NADH and oxaloacetate are reduced, and reverse Krebs cycle reaction is catalyzed by malate dehydrogenase, regenerating NAD^+ , thereby maintaining the production of ATP [11].



Figure 1. Scheme illustrating the main genes involved in tolerance to flooding at different plant development stages and potential advantages conferred to weeds. UFRGS, June 2020. RAmy3D (Rice α -amylases); SUS3 (sucrose synthase 3); OsTPP7 (trehalose-6-phosphate phosphatase); LDH (lactate dehydrogenase); ALDH (aldehyde dehydrogenase); ADH (alcohol dehydrogenase); PDC (pyruvate decarboxylase); OsB12D1 (named OsB12D1); NShB1 (non-symbiotic hemoglobins-B); TUB1A (tubulin α -1chain); ADF4 (actin factor 4); XETP (xyloglucan endotransglycosylase); SK1 (Snorkel1) SK2 (Snorkel2); SUB1A (*Submergence*-1).

2.2. Tolerance to Flooding during Seedling Emergence

When germinating under flood, the rice coleoptile has to elongate to reach the water surface to perform aerobic oxidative phosphorylation. Therefore, the emergence requirements have to be supplied quickly, before the energy reserves in the seed or vegetative propagules are exhausted [4]. Coleoptile elongation, and the speed at which it occurs, constitutes one of the ‘snorkeling’ strategies for flooding tolerance. Seedling emergence in flooded conditions is facilitated by ethylene-dependent responses [10]. In one study under flooded soil, ethylene was not detected in seeds of rice cultivars IR42 and FR13A not adapted to flooding at germination, but was abundant after germination in seedlings of the flood-tolerant genotype KHO [12]. The delay in ethylene production suggests that the source of ethylene is probably the embryos that grow under oxygen deficiency, being more related to post-germination growth rather than germination *per se* [12].

Ethylene acts as a stimulus for the mobilization of seed reserves after germination based on the activation of alpha-amylase enzymes [10][13]. Similar to what occurs in germination, high expression of the *Ramy3D* gene is

observed in the coleoptile and radicle of rice seedlings under anoxia (Figure 1). The expression of this gene was up to 592 times higher in the tolerant than in the susceptible genotype of rice at 8 d after seed imbibition [14]. Also associated with anoxia-tolerance in rice is the loci *OssTPP7* (Gene *OsTPP7*), which encodes the enzyme trehalose-6-phosphate, responsible for increasing the conversion of starch to glucose [15]. This gene was identified in the flooding-tolerant cultivated rice Khao Hlan On, but was absent in the susceptible cultivar IR64, implicating *OsTPP7* in flood tolerance [15]. The higher availability of sugar promoted the elongation of coleoptile, resulting in emergence and high tolerance to submersion [15][16]. Thus, these mechanisms enable seedling root and shoot growth of tolerant rice genotypes in flooded conditions. Tolerance to flooding during emergence of *Echinochloa* spp. Was linked to increased activity of LDH, ALDH, ADH, and PDC enzymes [17][10]. The growth of roots and shoots of flood-tolerant *E. crus-galli* was not affected by 100 mm depth of flood for 7 d after sowing [17].

Increased structural proteins and key enzymes have been related to continued coleoptile growth of rice seedlings under anoxia and may be the same factors involved in weed adaptation to flooding during emergence. The action of the tubulin α -1 chain (*TUBA1*) and actin factor 4 (*ADF4*) genes on the rapid elongation of coleoptile under anaerobic conditions has been proposed because both are upregulated under anoxia during rice emergence [18]. Tubulins enable cell division and elongation, as well as *ADF4*, is involved in the regulation of actin assembly [18]. Thus, increased expression of both genes in plants correlates with the superior ability to tolerate flooding during emergence (Figure 1). These findings indicate that there are two complex mechanisms of flooding tolerance during seedling emergence: (i) Increased mobilization of seed reserves and ii) the ability to maintain root and shoot growth during seedling emergence under flood.

2.3 Tolerance to Flooding during the Vegetative Stage

Flooding after the initial plant establishment elicits responses that differ across plant species and dependent on the speed and duration of flooding occurrence [5][10]. During initial growth, flooding stress-tolerant genotypes of rice can react by activating adaptation mechanisms to escape, or to withstand, flooding until the stress is alleviated by the formation of aerenchyma [19]. Although tolerance to flooding in rice is associated with aerenchyma, this mechanism of tolerance to flooding after establishment is also reported in other species, such as *Echinochloa* spp., *Sagittaria montevidensis*; *S. trifolia*, *Cyperus* spp., and *Rumex palustris* [4], or in flood-tolerant leguminous weeds of rice, such as *Sesbania herbacea* and *Aeschynomene virginica*. The presence of aerenchyma in flood-tolerant plants is also a snorkeling strategy. Aerenchyma is a plant tissue with a high proportion of intercellular spaces. The aerenchyma facilitates the diffusion of gases between the flooded and non-flooded organs of the plant, which allows the aerobic respiration of root cells [20]. The formation of aerenchyma in plants as a response to flooding is mediated by ethylene, inducing the activity of xyloglucan endotransglycosylase (*XETP*—Figure 1), which induces cell wall degradation. However, the formation of aerenchyma also requires reactive oxygen species (ROS) and Ca^{2+} in rice [21] and wheat [19]. In rice, ethylene or its precursor 1-aminocyclopropane-1-carboxylic acid (ACC) stimulates the formation of aerenchyma in roots [22].

The presence of aerenchyma alone does not guarantee the diffusion of O_2 to the root tips, because of radial oxygen loss (ROL). The rate of long-range oxygen diffusion from aerial shoots to the submerged roots is

maintained by a constitutive, or induced, an apoplastic barrier that prevents the ROL [22]. This barrier is typically composed of a suberized lamella that is formed in the exodermal/hypodermic space, near the tip of the root, and by lignified sclerenchyma/epidermal cells [10]. In this way, an efficient barrier is created that minimizes ROL and increases oxygen delivery to the root tip [19].

Genes encoding non-symbiotic hemoglobins (*NSHB1*) was observed in rice under flood conditions as a complementary mechanism for oxygen delivery to root tips, maintaining cell energy levels under conditions of hypoxia [23] (Figure 1). Hemoglobins react with nitric oxide (NO) produced under conditions of hypoxia, favoring an alternative route of respiration and transport of electrons in the mitochondria of plants under flood. Under hypoxia, NSHB1 reacts oxidatively with NO, producing nitrate and stimulating the consumption of NADH, thereby releasing NAD⁺ that can be reused in glycolysis [23]. These mechanisms, acting alone or concomitantly, certainly occur in flooding-tolerant weeds. However, the specific function in different species is not known.

Aerenchyma formation is crucial in cases of complete submersion of the plant, but aeration is more efficient when the aerial part can grow above the water level [24]. Some plant species growing in flooded environments have evolved the ability to elongate porous shoots under flooded conditions to facilitate the uptake of oxygen from the atmosphere and to transport it to the roots via the aerenchyma. This adaptation has a high energy cost and is restricted to native species in environments characterized by shallow, but prolonged flooding [25]. These flood-adapted plants possess the mechanism described as low O₂ escape syndrome (LOES), which is observed in some rice varieties and *Rumex palustris* [26].

The submersion escape mechanism is activated by low oxygen concentration and promoted by ethylene, gibberellic acid, and auxin, which collectively promote underwater growth and stretching [27]. The modulation of the response to flooding in rice is a function of the *SNORKEL* (SK) locus, responsible for stem elongation under deep water [28] (Figure 1). This locus encodes two ethylene-inducible transcription factors, group VII (Ethylene Response Factor (ERF): *SK1* and *SK2* [10]. The expression of these genes promotes elongation of the rice internodes, enabling plants to elongate underwater at a rate of 25 cm d⁻¹ in the flood-tolerant variety C9285 [28]. The signaling effects of *SK1* and *SK2* on the downstream events, which culminates in plant elongation is unclear, but act on GA biosynthesis [25]. The expression of the gene *SK1* was associated with flooding tolerance in ITJ03 weedy rice genotype and was not observed in flood-sensitive rice cultivars IRGA 417 [3].

The escape response to flooding is beneficial if the plant reaches the surface of the water before the plant dies. This is a high-energy-cost strategy and could exhaust the plant's carbon reserves before emergence from deep flood [26]. Thus, some species have evolved another mechanism of flood tolerance based on low O₂ quiescence syndrome (LOQS), which was identified in local rice cultivars from Asia [27]. This tolerance mechanism also involves ethylene, with the *SUB1* locus encoding two to three ERF-VIIs, including *SUB1A*, which regulates metabolism and extends the rice survival under complete submersion to up to two weeks, as well as their recovery and regrowth after the stress ends [26]. Ethylene is accumulated up to saturation level in the plant under flooding, but the ABA and GA concentrations are constant. This tolerance mechanism is also present in the weed *Rumex acetosa*, exhibiting metabolic adjustments consistent with energy conservation [29]. In this way, the growth of the

petiole and other energy-demanding processes are suppressed, allowing the conservation of resources until the flood recedes [25].

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