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Rice growth adapting to deepwater

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Flooding is one of the most hazardous natural disasters, and there are several levels of flooding. Recently, research on flood-tolerant rice plants revealed that some rice varieties have evolved to overcome two different flood types, 'flash flood' and 'deepwater flood', using two different mechanisms, and their molecular mechanisms were determined. During flash flooding, the tolerant plants that are fully submerged for a few weeks stop elongating and thus avoid energy consumption that will be needed to restart growth when the water recedes. On the contrary, during deepwater flooding, with water depth up to several meters for several months, the deepwater-flood-tolerant rice plants promote elongation of internodes to keep the foliage above the water surface and thus allow respiration and photosynthesis.

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Introduction

There are many different environments on Earth, some of which constitute severe and adverse environmental conditions for living organisms. Therefore, living organisms have developed many biological functions to overcome such severe environmental conditions and have succeeded in adapting to many unfavorable environments. Unlike motile organisms, plants are sedentary and cannot move rapidly in response to sudden environmental changes. Thus, plants must face environmental alterations directly and establish new adaptation mechanisms to overcome hostile environments. At the same time, plants must expand their habitats for the continuation of their species and avoiding competition with other species. Over their long evolutionary history of habitat expansion, plants have faced many kinds of severe environmental conditions, such as deserts, brackish-water

regions, high altitude and hot or cold climates. Over this long time, plants have evolved through natural selection, gaining new adaptations and increased diversity, and have succeeded in expanding their habitats.

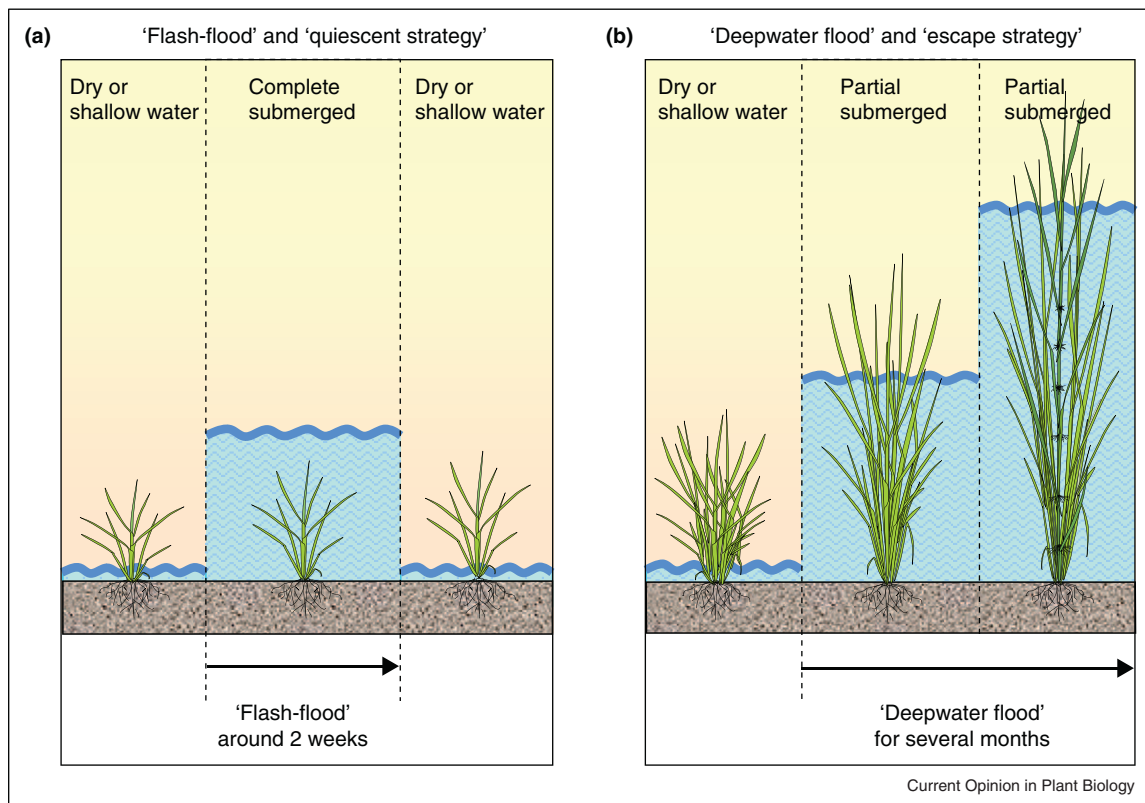
Water is essential for all life, and living in a watery environment, such as rivers, lakes and swamps, can be an advantage for plants and animals. However, living beside water also involves the risk of sudden flooding or long periods of flooding after heavy rain. Flooding is a natural disaster which causes growth inhibition and great reduction of yield. Common rice (*Oryza sativa* L.) cultivars are generally planted in dry or irrigated areas, and are comparatively tolerant to water compared to other crop plants, such as maize and wheat [1]. However, rice does not have complete tolerance to flooding, and if it is completely submerged or flooded for long periods, plants die due to oxygen starvation and energy depletion [2]. Flooding levels vary, depending on the amount and duration of rain, underlying geological formations and distance from the water. Among these factors, there are two typical kinds of flood. One is short duration over a few weeks and not very deep, termed a 'flash flood' (Figure 1a) and the other is deep flooding that lasts for a long time, a 'deepwater flood' (Figure 1b). Recent studies have revealed that rice plants have adapted to these two forms of flooding through different tolerance mechanisms (Figure 1).

Many agronomic traits, including tolerance to flash and deepwater floods, are expressed in continuous phenotypic variations. These complex traits are generally governed by some or many genes, that is quantitative trait loci (QTL), derived from natural variations in the plant [3,4]. QTL analysis has been used as a powerful tool to discover complex traits and help in the initial step of cloning the genes [5–9]. Progress in obtaining genomic information as well as new tools [10,11] has greatly facilitated QTL analysis in rice. In this review, we focus on rice avoidance and elongation strategies, and discuss the molecular mechanisms involved.

Quiescence under flash flood

Tolerance to flash flood (i.e. submergence tolerance) is defined as 'the ability of a rice plant to survive 10–14 d of complete submergence and renew its growth when the water subsides. . . ' [12[•]]. Flash floods are unexpected and uncontrollable, and its flooding water level can reach 50 cm in the rain-fed lowlands of the humid and semi-humid tropics of South and Southeast Asia. In these areas, flash floods at the seedling stage of rice cause severely reduced yields of rice grain [12[•]]. However, some rice

Figure 1



Two strategies used by rice in response to two different kinds of flooding. **(a)** The 'quiescent strategy' for flash flooding. Rice plants tolerant to flash flooding have stunted growth under submerged conditions. Flash floods generally completely submerge the plants and last about two weeks. After the floodwater recedes, flash-flood-tolerant rice restarts growth. **(b)** The 'escape strategy' for deepwater flooding. Rice plants tolerant to deepwater flooding, where water depth is from 50 cm to around 4 m, show significant stem elongation as water levels rise. Deepwater floods occur annually, in the rainy season, and last for several months. After the floodwater recedes, the deepwater-flood-tolerant rice becomes flattened, and generates new roots and tillers [12*].

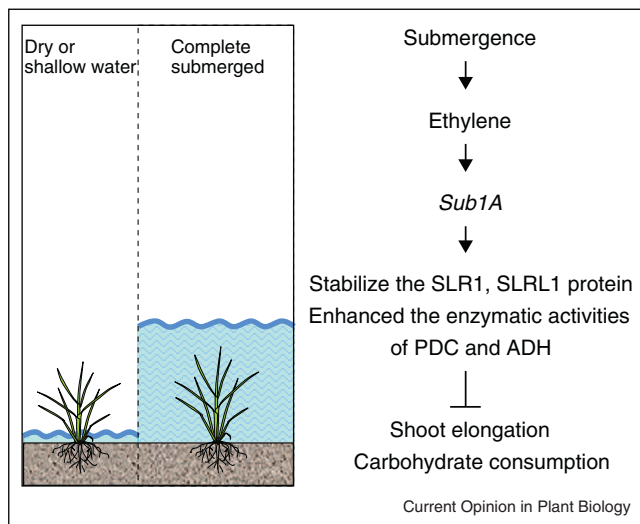
strains show flash-flood tolerance (submergence tolerance) and survive such floods. Recently, the gene responsible for this tolerance was identified thus suggesting its molecular mechanism (Figure 2).

The genetics of flash-flood tolerance have been studied since the 1980s – it is controlled by a few genes that are partially or completely dominant [13]. Analyses of flash-flood tolerance confirmed that the QTL on chromosome 9 has the strongest effect, accounting for 69% of the phenotypic variation [14]. QTL analysis and positional cloning allowed the identification of the *Submergence1* (*Sub1*) locus on chromosome 9, which confers submergence tolerance [15*,16**]. In this locus, there are three similar genes that encode an ethylene response factor (ERF)-type transcription factor domain: *Sub1A*, *Sub1B* and *Sub1C*. These three genes are located in tandem with submergence-tolerant varieties. By contrast, some submergence-intolerant varieties possess only *Sub1B* and *Sub1C*, but lack *Sub1A*. The introduction of *Sub1A* of submergence-tolerant strain into submergence-intolerant

varieties leads to submergence tolerance. These results indicate that *Sub1A* is the most effective of the three submergence-tolerance genes [15*,16**] (Figure 2).

Rice plants carrying *Sub1A* show restricted growth under submerged conditions, and thus avoid energy consumption associated with plant elongation. After the floodwater recedes, such plants can restart growth using the conserved energy. During submergence, higher induction of α -amylase genes (*RAmy3C*, *RAmy3D* and *RAmy3E*) and sucrose synthase genes (*Sus1*, *Sus2* and *Sus3*) were observed in submergence-intolerant plants; by contrast, there was lower expression of these genes under the same conditions in submergence-tolerant plants [16**]. Rice α -amylases function during rice germination, breaking down starch into sugars, and accumulate in the seed embryo and aleurone cells, even under anoxia [17]. Sucrose synthase genes also show increased expression under low-oxygen conditions in maize roots and potato tubers [18,19]. These results suggest that *Sub1A* negatively regulates transcription of these genes, to reduce

Figure 2



Molecular mechanism of the 'quiescent strategy'. The flash-flood-tolerant rice (submergence-tolerant rice) grows under dry or shallow water conditions. At the seedling stage, sudden floods can completely submerge the plants. During submergence the ethylene-responsive gene, *Sub1A*, is upregulated. Additionally, the enzyme activities of PDC and ADH, and the stability of SLR and SLRL1 proteins, are enhanced. As a result, shoot elongation and carbohydrate consumption is repressed under submerged conditions.

energy consumption during submergence. Additionally, ethanolic fermentation is necessary during low-oxygen and submergence stress [20,21], and pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH) genes are increased under low-oxygen conditions. Both enzymes function in the ethanolic fermentation pathway. Expressions of two *PDC* genes and two *ADH* genes are induced during submergence in submergence-tolerant rice [16^{••}]. This suggests that *Sub1A* positively regulates the expressions of *PDC* and *ADH* genes under hypoxia. The flash-flood tolerance gene, *Sub1A*, would promote acclimation to low-oxygen conditions by regulating expression of these genes (Figure 2).

Plant growth is controlled by the accurate regulation of plant hormones, even during growth under flooded conditions. During flash floods, submergence-tolerant lines limit their growth through the gibberellic acid (GA) signal transduction pathway [22[•]]. Slender rice-1 (SLR1) and SLR1-Like-1 (SLRL1) are repressors of GA signaling. SLR1 and SLRL1 proteins accumulate during submergence in submergence-tolerant rice, but not in submergence-intolerant rice. These results indicate that the restricted growth of submergence-tolerant rice is caused by the accumulation of SLR1 and SLRL1, which repress the GA signal through *Sub1A* [22[•]] (Figure 2). The transcriptome analyses revealed that further to the above factors, some complex events may exist downstream of

Sub1A, such as cytokinin response and detoxification of reactive oxygen species [23].

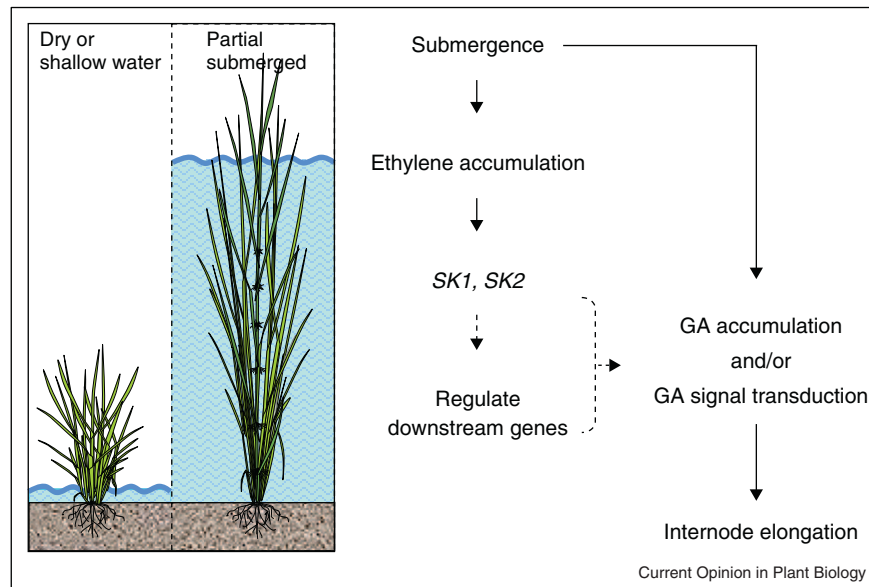
Escape from deepwater flood

Deepwater rice is cultivated around river basins or delta areas in South and Southeast Asia, West Africa and South America, such as in the Mekong, Ganges, Brahmaputra, Amazon and Niger deltas, where severe floods occur in the rainy season every year, and where water levels can reach several meters. Furthermore, these deepwater floods can last for several months, depending on the amount and duration of precipitation. In these areas, few plants can survive under the long-term deepwater-flood conditions, even the flash-flood-tolerant rice. However, deepwater rice varieties can survive, because of rapid stem elongation with rises in water level, sustained by internode elongation [12[•]]. Ordinary paddy rice cultivars do not initiate internode elongation during the vegetative stage; however, deepwater rice cultivars can elongate internodes even in early growth stages and also develop aerenchyma, the snorkel-like conduits in internodes that allow gaseous exchange. This remarkable internode elongation occurs during seasonal flooding, reaching depths up to several meters, and deepwater rice has growth with daily increases in plant height of 20–25 cm; ultimately, plants can reach a height of 7 m, in contrast to only 1.5 m when grown in dry or shallow water condition [12[•],24]. Thanks to these unique characteristics, deepwater rice can respond to rising water levels and start internode elongation to keep the top leaves above the water surface and avoid oxygen starvation. These characters allow such cultivars to survive deepwater flood, and deepwater rice cultivars are an important crop in flood-prone areas (e.g. Bangladesh, Thailand and Cambodia) [25]. Furthermore, deepwater rice provides valuable material for studying culm elongation [26[•]] and the genetic elements involved in phenotypic plasticity [27]. Apart from these characteristics and comparatively low yields, deepwater rice does not show any significant difference to ordinary paddy rice under dry or shallow water conditions [28].

Morphological and physiological analysis of internode elongation of deepwater rice under deepwater conditions involves the phytohormones: ethylene, abscisic acid and gibberellic acid (GA) [26[•]]. Among them, ethylene functions as an initiation factor for internode elongation [29,30]. Molecular and biological approaches have shown that expression of several deepwater rice genes is regulated in response to water level [31–39]. However, the exact trigger(s) for rapid internode elongation remain(s) unknown.

A classic study on the inheritance of deepwater characteristics was performed by Ramiah and Ramaswami, who showed that internode elongation was controlled by duplicate genes, designated *ef1* and *ef2* [40]. Hamamura

Figure 3



Molecular mechanism of the 'escape strategy'. When the deepwater-flood-tolerant rice (deepwater rice or floating rice) is submerged, it elongates leaves and internodes as the water rises and keeps the foliage above the water surface. In the flooded parts of the plants, ethylene is physically trapped and its content becomes elevated. This accumulated ethylene induces expression of *SK1* and *SK2*, which function as ERF-type transcription factors, through binding with EIN3. Additionally, the amount of GA is increased under flooded conditions. *SK1* and *SK2* may act directly or indirectly to promote GA biosynthesis and/or GA signal transduction, followed by ethylene accumulation. GA positively regulates elongation of leaves and internodes.

and Kupkanchankul performed diallel crosses and analyzed the progeny [41]. They reported that the ability of rice to float was a partially dominant characteristic, and further analysis showed that approximately five or six genes were involved in the floating ability. Tripathi and Rao reported that early nodal differentiation, a typical feature of deepwater rice, is controlled by a single dominant gene [42], whereas Suge reported that internodal elongation in deepwater rice can be explained by the presence of complementary genes [43]. Eiguchi *et al.* reported that internode elongation in deepwater rice was associated with a single recessive gene, *dw3* [27]. In more recent times, with the development of QTL analysis, the deepwater response has been suggested to be a quantitative trait regulated by QTLs [14,44–50].

In 2009, Hattori *et al.* identified the QTL that had the strongest effect; the *SNORKEL1* (*SK1*) and *SNORKEL2* (*SK2*) are located on chromosome 12, according to positional cloning [51••]. Transgenic non-deepwater rice plants with *SK1* and *SK2* show internode elongation in response to deepwater, and ectopic over-expression in non-deepwater rice of *SK* genes driven by the rice actin promoter resulted in internode elongation even in dry conditions. These results suggest that *SK* genes positively regulate internode elongation. These two *SK* genes encode putative ERF that are thought to be ERF-type transcription factors, possessing the single AP2/ERF

domain and a nuclear localization signal. Expressions of *SK* genes are significantly induced by ethylene treatment, but not by other plant hormones. As a result of subcellular localization analysis, using green fluorescent protein, *SK* proteins were found to localize in nuclei. Both proteins have transcription-activating abilities, according to analysis using a yeast one-hybrid system. Furthermore, the promoters of *SK 1* and *SK 2* can bind to rice ethylene-insensitive-3 (EIN3)-like protein (Figure 3). In Arabidopsis, EIN3 functions as a transcription factor in the ethylene-signal transduction pathway. These results suggest that *SK1* and *SK2* function as ERF-type transcription factors in ethylene signaling [51••]. They also show that GA is important for the deepwater response, although the relationship between ethylene and GA is still unknown (Figure 3).

Conclusions

Rice is a semi-aquatic plant and one of the most important crops cultivated in both tropical and temperate regions. More than half of the people on Earth depend on rice for their basic diet. Despite its importance, sudden or seasonal floods cause serious damage to rice crops and substantially reduce yields. During the rice evolutionary history, rice has developed adaptation mechanisms to withstand flooding and has developed a 'quiescent strategy' for flash flooding and an 'escape strategy' for deepwater flooding. These two strategies are used to

overcome reduced oxygen availability during flooding, and many researchers have studied the two strategies for a long time. However, no one identified the responsible genes because these mechanisms are controlled by QTL. In recent years, owing to the development of QTL analysis, *Sub1A* and *SK* genes were identified and their molecular functions were analyzed. These findings greatly contributed to the elucidation of molecular mechanisms for each strategy.

The ‘quiescent strategy’ involves stunted growth under complete submergence and saves energy, allowing regrowth after flooding; however, if flooding is prolonged, the plants will die from carbohydrate and energy deficiency. On the contrary, ‘escape strategy’ allows rice plants to access the atmosphere, exchange gases in respiration, and restart photosynthesis; however, this strategy needs massive amounts of energy. Rice independently adapted and evolved these two contrasting strategies in response to local environmental conditions.

Interestingly, despite the two opposite behaviors, the underlying mechanisms are controlled by ERF-type transcription factors, which involved in the ethylene signal transduction pathway, and GA. However, the precise mechanisms of adaptation to deepwater are still unknown, such as how rice plants perceive the water level, and the relationship between ethylene and GA. Further analyses will reveal the novel mechanisms involved in adaptations to deepwater.

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