Available online at www.sciencedirect.com

SciVerse ScienceDirect

Current Opinion in Plant Biology

Genetic mechanisms conferring adaptation to submergence and drought in rice: simple or complex?

Takeshi Fukao[1] and Lizhong Xiong[2]

Both high and low extremes in precipitation increasingly impact agricultural productivity and sustainability as a consequence of global climate change. Elucidation of the genetic basis underlying stress tolerance facilitates development of new rice varieties with enhanced tolerance. Submergence tolerance is conferred by a single master regulator that orchestrates various acclimation responses, whereas drought tolerance is regulated by a number of small-effect loci that are largely influenced by genetic background and environment. Detailed molecular studies have uncovered the functional importance of genes and signaling components which coordinate various morphological and physiological responses to submergence and drought, providing new insight into understanding the complex regulatory mechanisms of stress tolerance in rice.

Addresses
[1] Department of Crop and Soil Environmental Sciences, Virginia Tech, Blacksburg, VA 24061, USA
[2] National Key Laboratory of Crop Genetic Improvement and National Center of Plant Gene Research, Huazhong Agricultural University, Wuhan 430070, China

Corresponding authors: Fukao, Takeshi (fukao@vt.edu) and Xiong, Lizhong (lizhongx@mail.hzau.edu.cn)

Current Opinion in Plant Biology 2013, **16**:196–204

This review comes from a themed issue on **Genome studies and molecular genetics**

Edited by **Qifa Zhang** and **Rod Wing**

For a complete overview see the Issue and the Editorial

Available online 28th February 2013

http://dx.doi.org/10.1016/j.pbi.2013.02.003

Introduction

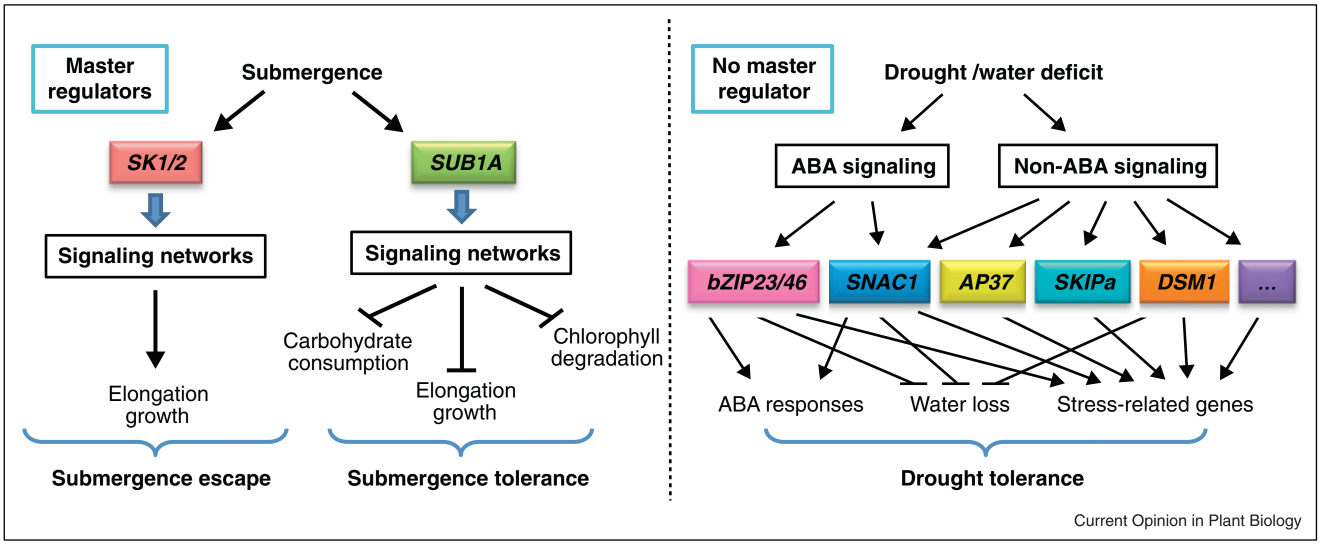
Global climate change alters frequency and intensity of precipitation and storms, causing unexpected flood and drought events in agricultural systems worldwide. Rice (*Oryza sativa*) is a semi-aquatic plant that is well-adapted to a partially flooded environment. However, prolonged complete submergence results in serious loss of grain yield in rainfed lowland fields. Drought is also a major constraint for rice production due to its high water requirement. To meet increasing food demand under changing environments, it is imperative to develop new rice varieties with enhanced stress tolerance in a timely manner.

Submergence dramatically alters availability of multiple environmental factors including oxygen, carbon dioxide, light, and nutrients, all of which are major components influencing primary anabolism and catabolism in plants. These environmental alterations trigger inhibition of photosynthesis and acceleration of energy reserve consumption, resulting in stunted growth or death. Rice cultivars show a range of growth responses to submergence. Deepwater rice rapidly promotes gibberellic acid (GA)-mediated internode elongation under submerged conditions, enabling it to outgrow gradually rising floodwaters [1]. By contrast, a limited number of rice cultivars including FR13A can endure complete submergence for up to two weeks through restriction of carbohydrate consumption, chlorophyll degradation, and elongation growth [2,3]. Interestingly, two antithetical adaptive responses, escape versus quiescence, are primarily governed by the multigenic *SNORKEL* (*SK*) and *SUBMERGENCE-1* (*SUB1*) loci, respectively, both of which encode tandem-repeated *ETHYLENE RESPONSIVE FACTOR* (*ERF*)-type transcription factor genes (Figure 1). Functional characterization of these *ERF* genes has expanded our understanding of the mechanisms that control various morphological and physiological responses to submergence [1–4].

Water deficit influences numerous biological pathways and processes in plants, which triggers various developmental and physiological responses. To date, hundreds of loci that affect these adaptation responses have been estimated by quantitative trait loci (QTL) analyses in rice [5–8,9••,10]. However, only a limited number of loci have been validated for their functions in drought tolerance using marker-assisted selection [11,12•,13]. Dehydration stimulates accumulation of abscisic acid (ABA) in vegetative tissue, which promotes stomatal closure, stress-related gene expression, and metabolic adjustment to enhance adaptability to the stress [14]. Genome-scale gene expression analyses have identified genes that are highly induced in response to dehydration and ABA [15–18]. It has been confirmed that overexpression or knockdown of each of the representative dehydration and ABA-inducible genes significantly influences tolerance to drought due to proper regulation of ABA responsiveness, water loss, and stress-related gene expression [19••,20,21•,22–24] (Figure 1). However, unlike submergence responses, it does not appear that drought tolerance is largely controlled by a single master regulator in rice.

In this review, we contrast genetic analyses of tolerance to two opposing water stresses in rice, featuring the efforts and challenges in genetic dissection of the complex

Figure 1



Genetic regulation of submergence and drought tolerance in rice. Rice can overcome submergence stress through antithetical growth responses, escape versus quiescence, which are primarily controlled by group VII *ERF* genes, *SK1/2* and *SUB1A*, respectively. By contrast, drought tolerance is governed by a number of small-effect genes that regulate various acclimation responses to the stress. Most of these genes encode transcription regulators (e.g. *bZIP23*, *bZIP46*, *SNAC1*, *AP37*, *SKIPa*) or protein kinases (e.g. *DSM1*), acting mainly through ABA-dependent or ABA-independent signaling pathway.

regulatory mechanisms underlying submergence and drought tolerance. We also highlight recent advances in understanding the functional roles of genes, signaling molecules, and their interactions in the regulation of adaptation responses to the two water-related stresses.

Genetic bases of submergence responses and tolerance in rice

Abiotic stress tolerances are complex traits that comprise various morphological and physiological processes regulated by multiple genes. However, certain stress tolerances can be governed by a single master regulator, which orchestrates complicated stress responses at various levels. One example is the *SUB1* locus which coordinates chlorophyll degradation, carbohydrate consumption, amino acid accumulation, and shoot elongation, all of which are key responses to enhance submergence adaptation [2,4,25••,26]. Notably, multiple QTL analyses have identified the *SUB1* locus (phenotypic variance 41–77%) in diverse mapping populations and growth conditions [27–30]. *SUB1*'s enhancement of submergence tolerance is highly penetrant based on transfer of the trait to a number of high-yielding cultivars through marker-assisted selection [31–33]. Besides submergence tolerance, low phosphate tolerance and low temperature germinability are also conferred by a single large-effect QTL [34,35], which are immediate targets for rice breeding programs.

The *SUB1* locus encodes a variable cluster of two or three tandem-repeated group VII *ERF* genes [3]. All *O. sativa* accessions contain *SUB1B* and *SUB1C* genes, whereas *SUB1A* is present in limited *indica* and *aus* cultivars. Extensive surveys of diverse rice accessions have demonstrated that submergence tolerance is associated with pronounced submergence-inducible expression of *SUB1A* [3,36]. Interestingly, rapid underwater elongation (submergence escape) in deepwater rice is also primarily regulated by the locus that contains tandem-repeated group VII *ERF* genes, designated *SNORKEL 1* (*SK1*) and *SNORKEL 2* (*SK2*) [1]. In addition, the presence of *SUB1A* and *SK* genes correlates with submergence tolerance and escape, respectively, in *O. rufipogon*, a wild relative of cultivated rice [1,37], indicating that the functional roles of these *ERF* genes in submergence responses are conserved within the AA genome *Oryza* species.

Physiological and molecular characterization of *SUB1A* and *SK* genes have revealed that these *ERF VII* genes regulate antithetical growth responses to submergence through similar hormonal pathways (Figure 2). Transcript accumulation of both *SUB1A* and *SKs* is induced in response to ethylene accumulated under submerged conditions [1,2]. In deepwater rice, *SK1*, *SK2* and two minor QRLs augment accumulation of bioactive GA in submerged internodes, promoting GA-mediated underwater elongation to outgrow floodwaters. In submergence-tolerant rice varieties, ethylene-induced accumulation of *SUB1A* mRNA ultimately limits ethylene production during submergence. *SUB1A* also dampens responsiveness to GA through upregulation of SLR1 and SLRL1,