J. Plant Biol. (2011) 54:365–372
DOI 10.1007/s12374-011-9182-7

REVIEW

Molecular Events Underlying Coordinated Hormone Action in Submergence Escape Response of Deepwater Rice

Dongsu Choi

Received: 4 September 2011 / Accepted: 7 September 2011 / Published online: 20 September 2011

Abstract Recent studies revealed that some rice varieties adopt opposite strategies to overcome flooding stress. While certain varieties hold metabolism and stay stunted until floodwater recedes, deepwater rice varieties undergo rapid stem elongation and do not suffer drowning problems. Both varieties use the same signaling agents, the ethylene response factors, as key factors even though they display opposite submergence responses. In deepwater rice, ethylene response factor genes *SNORKEL1* and *SNORKEL2* are believed to play a major role in submergence escape by mediating ethylene signaling, which leads to rapid stem elongation. These genes connect hormone signaling cascades from ethylene to ABA and gibberellins (GAs). Submergence increases ethylene levels in the internodal space, ethylene upregulates an ABA inactivating enzyme gene, *OsCYP707A5* or *OsABA8ox1*, and some GA metabolism genes such as *OsGA20ox* genes and *OsGA3ox* genes. As a result of gene regulation by ethylene, internodal ABA levels decrease while GA levels increase, finally upregulating growth-related genes like expansin genes (*OsEXPs*). Along with the ethylene signaling in submergence, it is necessary to consider an alternative signaling pathway induced by hypoxia. Taken together, study on the submergence responses of rice plants will lead to improvement of crop production and contribution to basic research on plant growth.

Keywords Submergence escape · Submergence tolerance · Ethylene · Gibberellins · ABA · Hypoxia

D. Choi (✉)
Department of Biological Science, Kunsan National University,
Gunsan 573-701, Korea
e-mail: choid@kunsan.ac.kr

Introduction

In the twenty-first century, global climate change is rising as a major issue in agriculture as well because it will affect crop cultivation as the sea level ascends, flooding lowland fields, and as local heavy rains occur frequently, increasing the flooding rate of rivers (Fedoroff et al. 2010). Frequent or prolonged flooding usually deals severe damage to plants because excess water in their environments will limit the supply of important elements for their survival, such as oxygen, carbon dioxide, and light for photosynthesis (Jackson et al. 2009). Thus, flooding is one of the major abiotic stresses on crop distribution and agricultural productivity worldwide. As most crop plants are sensitive to submergence, frequent and prolonged flooding is considered a main threat to crop production. To overcome the problems caused by flooding, it is reasonable to study how certain plant species tolerate or avoid submergence stress.

Rice is a semiaquatic species that adapts well to water-filled environments. Since water levels of rice fields vary according to location and climate, some rice varieties have to take extreme strategies to survive adverse conditions they are faced with.

In general, most rice varieties are sensitive to continuous and complete submergence. In fact, with limited exceptions, rice plants submerged for more than a week do not survive mainly because of oxygen deficiency. To avoid the detrimental effects of submergence, rice plants have developed two opposite strategies. Rice varieties well adapted to submergence stress are either more resilient against or capable of escaping submergence stress. Rice varieties with the resilience strategy can hold their metabolism for up to 2 weeks under complete submergence, reverting back to normal growth when floodwater recedes, by which they have the trait of submergence tolerance. On the other hand, other rice varieties, namely deepwater or floating rice, adopt an escape strategy that can secure the routes for oxygen supply by rapid stem growth, enabling them to stick their foliage parts out of the floodwater (Jackson 2008).

During the last three decades, studies on the physiological aspects of stem elongation in submerged deepwater rice have accumulated quite a bit of evidence on hormone interactions to mediate submergence stimulus and actual plant growth (Kende et al. 1998). Nevertheless, the major factors to sense submergence stress and the agents to regulate downstream signaling cascades for the tolerance or escape responses to submergence have not been identified.

Recently, two groups of scientists clearly demonstrated that ethylene signaling pathways are a key factor for both submergence tolerance and escape strategies. In submergence-tolerant rice varieties, shoot elongation does not occur, and the plant consumes minimal carbohydrates because Sub1A, an ethylene response factor, represses GA responses (Xu et al. 2006; Fukao and Bailey-Serres 2008). Contrarily, certain deepwater rice varieties undergo rapid internodal elongation mainly by activation of SNORKEL1 (SK1) and SNORKEL2 (SK2), two other ethylene response factors that stimulate GA responses in intercalary meristem (Hattori et al. 2009).

In this review, we will discuss in detail the importance of hormone action and molecular events responsible for submergence escape. Furthermore, we will also address the importance of hypoxia-related signaling as well as ethylene-dependent molecular events in submergence escape behavior of deepwater rice. Taken together, we propose a new model for submergence escape, one that emphasizes ethylene-independent signaling pathway initiated by hypoxia.

Physiology and Hormone Interaction under Submergence Stress: Submergence Tolerance vs. Submergence Escape

Plant development and growth is mainly regulated by the integrated action of various hormones. In shoot apical meristem, for example, the integration of hormone signaling, such as that of cytokinins and GAs, is critical in maintaining meristematic identity (Kepinski 2006). Likewise, at least three hormones (ethylene, ABA, and GAs) interact and integrate their signals to avoid submergence stress (Kende et al. 1998; Azuma et al. 2003; Voesenek et al. 2003; Xu et al. 2006).

Plants usually show signs of detrimental stress from two different types of flooding: flash floods and long-lasting deepwater floods. Some adaptive indica rice cultivars show submergence-tolerance response in a flash flood by holding carbohydrate metabolism at the lowest level, whereas deepwater rice cultivars actively use a submergence escape strategy by rapid stem growth (Nagai et al. 2010). As a result, submergence-tolerant cultivars remain stunted for a few weeks of submergence and restart growth by consuming saved energy after the floodwater recedes.

FR13A, a submergence-tolerant cultivar, is able to survive complete submergence for up to 2 weeks. It is known to acquire submergence tolerance by at least three separate processes. As the first process for submergence tolerance, the FR13A plant stops consuming carbohydrates upon submergence, which results in energy preservation and stunted growth as mentioned above. With the saved energy, it resumes normal growth as floodwater is gone. De-submergence (exposure to air) after prolonged submergence rapidly increases reactive oxygen species (ROS), causing fatal damage to submergence-sensitive species. To survive such oxidative stress during de-submergence, plants require antioxidant defense systems. Thus, it is plausible that high levels of antioxidant enzymes are active in submergence-tolerant lines during the process of de-submergence, while the enzyme levels are low in submergence-sensitive or submergence-avoiding lines or cultivars (Jung et al. 2010). As the second process, submergence-tolerant lines are well equipped with an antioxidant defense system which mitigates damage caused by elevated level of ROS during de-submergence process. Recently, it has been reported that ROS accumulation is not the only detrimental event occurring in de-submergence. Vegetative tissues including leaves have been found to undergo dehydration during de-submergence (Fukao et al. 2011). Finally, as the third process, submergence-tolerant lines also have increased responsiveness to ABA leading to efficient acclimation to dehydration. In fact, ethylene is the first hormone to regulate initial physiological events including intricate interaction with GA and ABA in submergence tolerance response.

In the case of submergence escape response, a number of data regarding hormone metabolism and interaction have been accumulated. The main response to accomplish submergence escape is rapid elongation of stems or shoots. The physiology of submergence escape is well studied in deepwater rice. When deepwater rice is submerged partially, a continuous stream of air layers is formed throughout the leaf blades and acts as the major route for air supply (Raskin and Kende 1983). This is possible because rice leaf blades are covered with hydrophobic epidermis which denies being soaked with water and eventually creates water-free zones between leaf surfaces and water. As the water level increases, gas composition inside intermodal lacunae changes dramatically. Oxygen level rapidly decreases by up to 3% (v/v) to make lacunae hypoxic, while partial pressures of CO_2 and ethylene increase up to 6% (v/v) and 1 μL L^{-1}, respectively (Raskin and Kende 1984; Stünzi and Kende 1989). Maintenance of oxygen level in lacunae is attributable to photosynthetic activity and supply from air channels formed in leaf blades. Because of low diffusion coefficient of ethylene in water, the gas is trapped in lacunae while ethylene production continues, which leads to a rapid increase in ethylene concentration in intercalary meristem region. Increased levels of ethylene subsequently affect concentrations of two adverse hormones, ABA and GAs. In rice, ABA and GA act antagonistically as known in seed germination and coleoptiles growth. This is the case in internodal growth of deepwater rice. In the presence of higher levels of ethylene, the ABA content is reduced by 75% whereas the GA_1 level is elevated up to four-fold (Hoffmann-Benning and Kende 1992). As a result, responsiveness of intercalary tissue to GA is greatly enhanced, resulting in activation of GA-inducible genes responsible for cell growth and division (Fig. 1). However, it is not likely that all hormones and environmental signals work together simultaneously. Growth experiments using excised deepwater rice stem revealed that hypoxia occurs first before the ethylene response that precedes GA action in the intercalary meristem (Fig. 2). Therefore, GA is considered to be the ultimate plant hormone that promotes elongation of deepwater rice internodes. GA_1 is also known to induce ethylene production in deepwater rice internodes (Azuma et al. 1994), indicating synergistic interaction between ethylene and GA. Hormone interaction during submergence response has also been confirmed in the flooding-tolerant dicotyledonous model plant *Rumex palustris* (Voesenek et al. 2003). Therefore, as in submergence tolerance, ethylene also initiates major physiological changes in submergence escape response by interacting with GA and ABA.

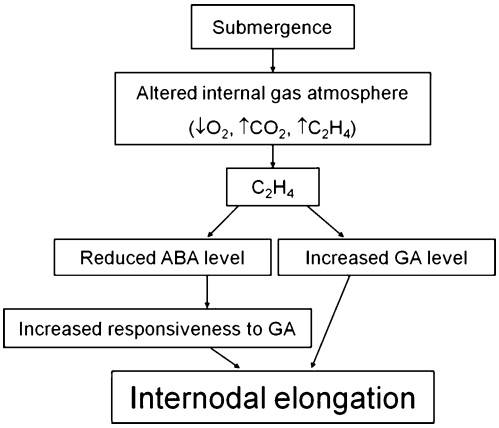

Fig. 1 Physiological events during submergence-induced intermodal elongation in deepwater rice

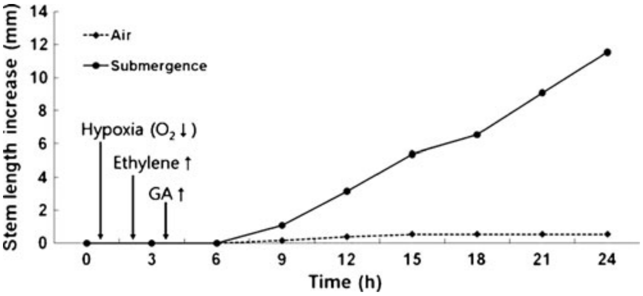

Fig. 2 Growth of deepwater rice stems under submergence. Hypoxia occurs within 30 min from the beginning of submergence. Increases in ethylene and GA levels subsequently follow hypoxia no later than 2 h and 4 h, respectively

Ethylene Response Factors Play a Key Role Both in Submergence Tolerance and Escape

Submergence tolerance is tightly correlated with the expression of *sub1A* gene. *Sub1A* gene encodes an APETALA2/Ethylene Response Factor (AP2/ERF) DNA binding protein, which is responsible for ethylene signaling. Upon submergence, increased levels of ethylene promote expression of the *Sub1A-1* gene, resulting in positive regulation of GA repressors, Slender Rice 1 (SLR1) and SLR1-Like1 (SLRL1) (Fukao and Bailey-Serres 2008). As SLR1 and SLRL1 are negative regulators for GA action, activation of the proteins will lead to inhibition of GA action. At the same time, Sub1A inhibits ethylene biosynthesis (Fukao et al. 2006). As a result, submerged rice remains in quiescence holding shoot growth.

Recent report on the role of Sub1A using transcriptomic analysis revealed that Sub1A mediates activation of another 12 AP2/ERF transcription factor genes closely related to submergence tolerance. The putative functions of the transcription factors were classified into three categories: anaerobic respiration, negative regulation of ethylene-dependent gene expression, and negative regulation of GA-mediated shoot elongation (Jung et al. 2010). These reports confirmed the integrative role of Sub1A during submergence tolerance response.

Snorkel1 (*SK1*) and *Snorkel2* (*SK2*) genes encode two other AP2/ERF transcription factors that exist only in some wild rice varieties and deepwater rice cultivars. Interestingly, SK1 and SK2 share high similarity with Sub1A in their ERF domain. Based on the similarity in ERF domains, SK1, SK2, and Sub1A are included in the same clade of the ERF subfamily (Nagai et al.

2010). In spite of the structural similarity in ERF domain, SK1 and SK2 deliver opposite signaling compared with Sub1A. They are ethylene responsive and involved in initiating rapid stem elongation by promoting GA biosynthesis and responsiveness (Hattori et al. 2009). The reason why Sub1A and SKs have the opposite result under submergence stress is not clear. However, considering low similarity between full-length proteins (27.2% between SK1 and Sub1A, 27.4% between SK1 and Sub1A), it is likely that they interact with other proteins with different functions (Nagai et al. 2010).

Molecular Events Leading to Shoot or Stem Elongation during Submergence Escape

Ethylene Biosynthesis and Signaling

Submergence enhances the expression of a gene encoding 1-aminocyclopropane-1-carboxylate oxidase (ACO) and two genes for 1-aminocyclopropane-1-carboxylate synthase (ACS) in deepwater rice, indicating that ethylene biosynthesis can take place even in a low O_2 environment (Mekhedov and Kende 1996; Zarembinski and Theologis 1993, 1997).

Recently, a group of protein kinase, mitogen-activated protein kinase (MAPK), has begun to draw attention from the community of plant stress physiologists with respect of abiotic stress.

MAPKs, which comprise a large serine–threonine kinase family in higher plants, perform diverse biological roles in a variety of signaling pathways including responses to abiotic stress or hormone action in plant growth and development (Mishra et al. 2006). Five genes out of 17 rice MAPK genes were inducible by ethylene treatment (Rohila and Yang 2007), indicating MAPKs' critical role in ethylene-involved signaling pathways. Considering the importance of ethylene signaling in submergence responses, MAPKs may be crucial components of ethylene signaling both in submergence tolerance and escape response.

Ethylene and ABA Metabolism

For rapid stem elongation, the balance between the levels of ABA and GA is crucial. Therefore, it is necessary to look into ABA metabolism during submergence. The endogenous level of ABA is regulated not only by ABA catabolism but also by its biosynthesis. Recently, genes encoding ABA 8′-hydroxylase, a key enzyme in ABA catabolism, were identified and characterized in rice (Yang and Choi 2006; Saika et al. 2007). Deepwater rice has two *CYP707A* genes encoding ABA 8′-hydroxylase. Of the two *CYP707A* genes, only *CYP707A5* responds to ethylene treatment while CYP707A6 remains unchanged both in air and submergence (Yang and Choi 2006). This result suggests that *CYP707A5* is responsible for the inactivation of ABA in the presence of ethylene when deepwater rice is under partial submergence. A study on the shoot growth of a lowland rice (cv. Nipponbare) under submergence also showed that ethylene-promoted expression of *OsABA8ox1* gene (a counterpart of *CYP707A5* in Nipponbare) is critical in the ethylene-dependent regulation of ABA content (Saika et al. 2007).

Zeaxanthin epoxidase (ZEP) and 9-cis-epoxycarotenoid dioxygenase (NCED) are the major enzymes required to catalyze ABA biosynthesis (Xiong and Zhu 2003). In *Rumex palustris*, Benschop et al. (2005) found that the endogenous level of ABA decreases under submergence or in the presence of ethylene. In addition, they also demonstrated that ethylene represses expression of an ABA biosynthesis gene, *RpNCED*. Thus, ethylene-mediated suppression of ABA biosynthesis contributes in part to reduction in the endogenous ABA level. However, in seedling growth of lowland rice, ethylene did not strongly change the expression level of ABA biosynthetic genes, whereas submergence reduced the expression of the same genes (Saika et al. 2007).

A recent study also provides additional evidence that ethylene regulates the endogenous level of ABA by downregulating ABA biosynthesis genes in deepwater rice (Choi 2007). Therefore, it is evident that ethylene is one of the major factors that regulate endogenous ABA levels during submergence.

Ethylene and GA Biosynthesis

As shown in Fig. 2, GA is the ultimate hormone that can directly promote intermodal elongation. In deepwater rice, endogenous levels of GA_{20} increase in submerged internodes (Hoffmann-Benning and Kende 1992). As GA_1 is the active form of GA in rice, it is undisputable that increased levels of GA_1 are responsible for rapid internodal elongation. Ethylene also regulates endogenous levels of GA_1 by upregulating *OsGA20ox2* and *OsGA20ox4* genes encoding GA 20-oxidases, and *OsGA3ox2* gene encoding GA 3-oxydase. However, genes encoding GA 2-oxidase responsible for GA inactivation remained unchanged in the presence of ethylene (Choi 2007). Previous studies using *R. palustris* also demonstrated that long-term submergence-induced petiole elongation is mediated by elevated expression of *RpGA3ox1* gene encoding GA 3-oxydase (Benschop et al. 2006). As mentioned above, the balance between ABA and GA contents is important in rapid internodal elongation of deepwater rice. Consequently, ethylene plays the commander's role that controls endogenous levels of ABA and GA by differential regulation of biosynthesis genes of catabolism genes.

Activation of Factors for Cell Enlargement during Internodal Elongation

To accomplish rapid stem elongation, plants need to enhance water uptake and enlarge vacuolar spaces to generate sufficient turgor pressure for cell enlargement (Kende et al. 1998). A recent report demonstrated that some vacuolar proton pump and aquaporin proteins were activated and their gene expression level increased substantially upon submergence of deepwater rice (Muto et al. 2011). At the same time, the authors found that other aquaporin genes responsible for the transport of silicic and boric acids were downregulated under the same environment. As silicic and boric acids function to harden rice cell walls or to inhibit cell enlargement, it is plausible that these genes have to be downregulated to acquire rapid stem elongation.

Even if the cells in submerged tissues are ready to expand due to increased turgor pressure by activation of aquaporins and vacuolar proton pumps, the cell walls may still remain stiff enough to limit cell enlargement. To loosen the cell wall, it is crucial for the rigid cell wall structure to be relaxed. Among the cell wall proteins, xyloglucan endotransglucosylase/hydrolase (XTH) and expansins are responsible for the irreversible cell wall loosening under the influence of anoxia or ethylene (Ookawara et al. 2005).

Expansins are cell-wall-loosening proteins that can break rigid interlinks between cellulose microfobrils and matrix glycans. Expression study of rice expansin genes revealed that expression patterns of most expansin genes are tightly correlated to intermodal elongation by submergence or GA treatment (Cho and Kende 1997; Lee and Kende 2001, 2002). In addition, a series of research using transgenic plants provided solid evidence that expansins are required for regulating vegetative growth (Cho and Cosgrove 2000; Pien et al. 2001; Choi et al. 2003).

Hypoxia and a New Model for Submergence Escape with Emphasis on Ethylene-Independent Signaling

Even if ethylene signaling is considered a major factor for the rapid stem elongation in submergence escape response, it is necessary to investigate another critical factor: hypoxia.

Ethylene biosynthesis is generally inhibited in an oxygen-deficient environment because activity of ACC oxidase which catalyzes the final step in ethylene biosynthesis is O_2-dependent (Jackson 2008).

An *anaerobically inducible early* (*aie*) gene family was identified and characterized in FR13A. In FR13A and a submergence-sensitive indica variety IR34, there was no difference in *aie* gene expression under the submergence treatment. In addition, authors found that the expression level of an *aie* gene did not change in the presence of ethylene (Huq and Hodges 1999). These results indicate that *aie* gene is anoxia specific, but this gene alone may not be responsible for submergence tolerance. Because of its anoxia-specific expression, it is assumed that the *aie* gene plays a role in general anaerobic response under submergence.

Low levels of oxygen increase the activity of alcohol dehydrogenase (ADH; EC 1.1.1.1) and pyruvate decarboxylase (PDC; EC 4.1.1.1). A study on ethylene effect on maize roots and rice coleoptiles revealed that ethylene gives rise to morphological changes for efficient adaptations to oxygen deficiency but does not promote activities of ADH and PDC (Morrell and Greenway 1989). In addition, *ADH* gene expression in *Arabidopsis* showed that ethylene is needed in the expression of *ADH* gene but is not sufficient, which implies the presence of another factor for regulation of *ADH* gene (Peng et al. 2001). Therefore, it is possible that some factors related to hypoxia or anoxia regulate activities of ADH and PDC independently of ethylene.

Regarding the importance of ethylene biosynthesis under submergence, a study on *R. palustris* presented evidence that low level of ACC oxidase activity caused by reduction of oxygen level inhibits ethylene biosynthesis (Vriezen et al. 1999). In deepwater rice internodes, partial submergence creates a hypoxic environment rather than anoxia while prolonged complete submergence causes anoxia as the oxygen supply through air layers is blocked. As a result, anoxia reduces ethylene levels below physiological concentration. However, at least in rice internode, hypoxia maintains ACC oxidase activity at a low but sufficient level to initiate ethylene signaling. Thus, as long as deepwater rice is partially submerged, ethylene production is maintained at a low but enough rate for the signaling required for stem elongation. However, in a low oxygen environment (3% partial pressure), stem sections of deepwater rice were still able to accomplish rapid stem elongation compared to stem sections exposed to air even though the ethylene level in the internode was below the physiological concentration (Raskin and Kende 1984). In addition, by using AOA (aminooxyacetic acid) and $CoCl_2$ as inhibitors of ethylene biosynthesis, Azuma et al. (2001) confirmed that low levels (3%) of oxygen can promote intermodal elongation of deepwater rice without the influence of ethylene. Although, in both cases, the rate of intermodal elongation without ethylene was not as great as in the presence of ethylene, it is apparent that hypoxia by itself could initiate and promote stem elongation of deepwater rice.

Rice coleoptiles provide another example of ethylene-independent growth. Rice coleoptiles elongate faster in complete absence of oxygen than in air. A recent publication on transcriptomic profiling of rice seedlings suggests that expression levels of some expansin genes were remarkably high under anoxia (Lasanthi-Kudahettige et al. 2007). Considering that coleoptiles under anoxia may lack ethylene and that expansins are well-known cell wall proteins mediating cell growth, we can assume that some expansins enhance coleoptiles growth independently of ethylene under anoxia.

In submergence escape response of deepwater rice, hypoxia also plays as important a role as ethylene in intermodal elongation. Submergence creates hypoxic atmosphere in lacunae, and hypoxia subsequently stimulates ethylene biosynthesis initiating ethylene signaling. Meanwhile, hypoxia mediates ethylene-independent signaling by activation of hypoxia- or anoxia-inducible genes like *aie* genes. In the long run, diverged signaling of ethylene-dependent or ethylene-independent pathways may be integrated into increased GA responses completing submergence escape (Fig. 3).

Conclusion

Submergence escape response of deepwater rice is initiated by rapid change of gas composition inside lacunae, which promotes biosynthesis and accumulation of ethylene. Increased ethylene levels activate *SK1* and *SK2* genes, GA biosynthesis genes, ABA catabolism genes, and repress ABA biosynthesis genes (Hattori et al. 2011). ERF protein encoded by *SK1* and *SK2* genes may play a role in regulating GA and ABA metabolism genes, which eventually creates growth-ready environment in intercalary meristem of deepwater rice. Thus, it is evident that ethylene plays a central role in submergence-induced growth. As downstream of hormone signaling, some genes encoding vacuolar ATPase and aquaporins, and some GA-responsive genes like *OsEXPs* are rapidly activated, promoting cell growth to accomplish rapid intermodal elongation (Fig. 3). Even though important factors in submergence escape response have come to light in the context of ethylene signaling, factors related to hypoxia signaling remain unknown. As hypoxia without ethylene can still promote intermodal elongation, it is necessary to focus on hypoxia signaling to complete the model for submergence escape.

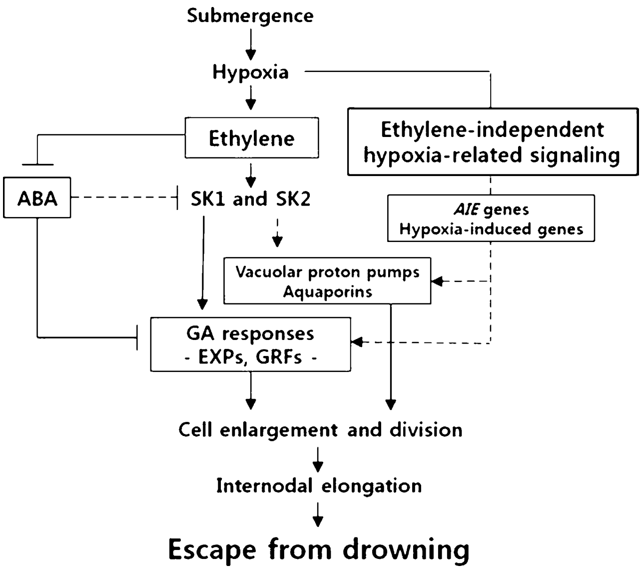

Fig. 3 Model for submergence escape response of deepwater rice. *AIE genes* anaerobically induced early genes, *EXPs* expansins, *GRFs* growth-regulating factors

In this review, in addition to the molecular analysis of submergence escape, we present a model emphasizing the importance of hypoxia along with ethylene signaling, which was never mentioned in the previous models for submergence escape.

Prospects

As global warming becomes eminent, flooding becomes more frequent and long lasting. Thus, submergence environment will more often play a negative role in crop production. Farmers will pay more attention to crop species with submergence tolerance or escape strategy to reduce the economic loss by flooding. Meanwhile, study on the submergence escape may give farmers the opportunity to save their efforts and money. Direct seeding, especially water seeding (seeds sown into standing water) may have an economic advantage over traditional transplanting in irrigated areas with good land leveling as it may save labor, mature earlier (shorter crop duration), reduce machinery operations, and avoid overuse of herbicides (Farooq et al. 2011). Nevertheless, the water seeding method is not prevalent worldwide because most rice varieties are sensitive to submergence. Understanding the mechanism of submergence escape may accelerate crop improvement suitable to water seeding and disseminate the water seeding method, which will eventually lead to reduction in rice production cost.

A number of data from the physiological research on plant growth and development suggest that plant hormones interact with one another to respond to external stimuli in most cases (Santner et al. 2009). As molecular biological and genomic research tools are under rapid development, we are able to find and analyze molecular components comprising hormone interactions. Therefore, with the explanation on the precise role of molecular components, it is valuable to build a submergence escape model for further understanding of hormone crosstalk in plant growth and development.

Acknowledgment This work was supported by a grant from the National Research Foundation of Korea (Code No. 2009–0072994) funded by the Korea government (MEST).

References

Azuma T, Hatanaka T, Uchida N, Yasuda T (2003) Interactions between abscisic acid, ethylene and gibberellins in intermodal elongation in floating rice: the promotive effect of abscisic acid at low humidity. Plant Growth Regul 41:105–109

Azuma T, Uchida N, Yasuda T (2001) Low levels of oxygen promote internodal elongation in floating rice independently of enhanced ethylene production. Plant Growth Regul 34:181–186

Azuma T, Uchida N, Yasuda T, Yamaguchi T (1994) Gibberellin-induced ethylene production in internodes of floating rice. Jpn J Trop Agr 38:78–82

Benschop JJ, Bou J, Peeters AJM, Wagemarker N, Gühl K, Ward D, Hedden P, Moritz T, Voesenek LACJ (2006) Long-term submergence-induced elongation in *Rumex palustris* requires abscisic acid-dependent biosynthesis of gibberellin$_1$. Plant Physiol 141:1644–1652

Benschop JJ, Jackson MB, Gühl K, Vreeburg RAM, Croker SJ, Peeters AJM, Voesenek LACJ (2005) Contrasting interactions between ethylene and abscisic acid in *Rumex* species differing in submergence tolerance. Plant J 44:756–768

Cho HT, Cosgrove DJ (2000) Altered expression of expansin modulates leaf growth and pedicel abscission in *Arabidopsis thaliana*. Proc Natl Acad Sci USA 97:9783–9788

Cho HT, Kende H (1997) Expression of expansin genes is correlated with growth in deepwater rice. Plant Cell 9:1661–1671

Choi D (2007) Ethylene-induced stem growth of deepwater rice is correlated with expression of gibberellin- and abscisic acid-biosynthetic genes. J Plant Biol 50:595–599

Choi D, Lee Y, Cho HT, Kende H (2003) Regulation of expansin gene expression affects growth and development in transgenic rice plants. Plant Cell 15:1386–1398

Farooq M, Siddique KHM, Rehman H, Aziz T, Lee D-J, Wahid A (2011) Rice direct seeding: experiences, challenges and opportunities. Soil Tillage Res 111:87–98

Fedoroff NV, Battisti DS, Beachy RN, Cooper PJM, Fischhoff DA, Hodges CN, Knauf VC, Lobell D, Mazur BJ, Molden D, Reynolds MP, Ronald PC, Rosegrant MW, Sanchez PA, Vonshak A, Zhu J-K (2010) Radically rethinking agriculture for the 21st century. Science 327:833–834

Fukao T, Bailey-Serres J (2008) Submergence tolerance conferred by *Sub1A* is mediated by SLR1 and SLRL1 restriction of gibberellins responses in rice. Proc Natl Acad Sci USA 105:16814–16819

Fukao T, Yeung E, Bailey-Serres J (2011) The submergence tolerance regulator SUB1A mediates crosstalk between submergence and drought tolerance in rice. Plant Cell 23:412–427

Fukao T, Xu K, Ronald PC, Bailey-Serres J (2006) A variable cluster of ethylene response factor-like genes regulates metabolic and developmental acclimation responses to submergence in rice. Plant Cell 18:2021–2034

Hattori Y, Nagai K, Ashikari M (2011) Rice growth adapting to deepwater. Curr Opin Plant Biol 14:100–105

Hattori Y, Nagai K, Furukawa S, Song XJ, Kawano R, Sakakibara H, Wu J, Matsumoto T, Yoshimura A, Kitano H, Matsuoka M, Mori H, Ashikari M (2009) The ethylene response factors SNORKEL1 and SNORKEL2 allow rice to adapt to deep water. Nature 460:1026–1030

Hoffmann-Benning S, Kende H (1992) On the role of abscisic acid and gibberellin in the regulation of growth in rice. Plant Physiol 99:1156–1161

Huq E, Hodges TK (1999) An anaerobically inducible early (aie) gene family from rice. Plant Mol Biol 40:591–601

Jackson MB (2008) Ethylene-promoted elongation: an adaptation to submergence stress. Ann Bot 101:229–248

Jackson MB, Ishizawa K, Ito O (2009) Evolution and mechanisms of plant tolerance to flooding stress. Ann Bot 103:137–142

Jung K-H, Seo Y-S, Walia H, Cao P, Fukao T, Canlas PE, Amonpant F, Bailey-Serres J, Ronald PC (2010) The submergence tolerance regulator Sub1A mediates stress-responsive expression of AP2/ERF transcription factors. Plant Physiol 152:1674–1692

Kende H, van der Knaap E, Cho HT (1998) Deepwater rice: a model plant to study stem elongation. Plant Physiol 118:1105–1110

Kepinski S (2006) Integrating hormone signaling and patterning mechanisms in plant development. Curr Opin Plant Biol 9:28–34

Lasanthi-Kudahettige R, Magneschi L, Loreti E, Gonzali S, Licausi F, Novi G, Beretta O, Vitulli F, Alpi A, Perata P (2007) Transcript profiling of the anoxic rice coleoptiles. Plant Physiol 144:218–231

Lee Y, Kende H (2001) Expression of beta-expansins is correlated with intermodal elongation in deepwater rice. Plant Physiol 127:645–654

Lee Y, Kende H (2002) Expression of alpha-expansin and expansin-like genes in deepwater rice. Plant Physiol 130:1396–1405

Mekhedov SI, Kende H (1996) Submergence enhances expression of a gene encoding 1-aminocyclopropane-1-carboxylate oxidase in deepwater rice. Plant Cell Physiol 37:531–537

Mishra NS, Tuteja R, Tuteja N (2006) Signaling through MAP kinase networks in plants. Arch Biochem Biophys 452:55–68

Morrell S, Greenway H (1989) Evidence does not support ethylene as a cue for synthesis of alcohol dehydrogenase and pyruvate decarboxylase during exposure to hypoxia. Aust J Plant Physiol 16:469–475

Muto Y, Segami S, Hayashi H, Sakurai J, Murai-Hatano M, Hattori Y, Ashikari M, Maeshima M (2011) Vacuolar proton pumps and aquaporins involved in rapid internode elongation of deepwater rice. Biosci Biotechnol Biochem 75:114–122

Nagai K, Hattori Y, Ashikari M (2010) Stunt or elongate? Two opposite strategies by which rice adapts to floods. J Plant Res 123:303–309

Ookawara R, Satoh S, Yoshioka T, Ishizawa K (2005) Expression of α-expansin and xyloglucan endotransglucosylase/hydrolase genes associated with shoot elongation enhanced by anoxia, ethylene and carbon dioxide in arrowhead (*Sagittaria pygmaea* Miq.) tubers. Ann Bot 96:693–712

Peng H-P, Chan C-S, Shih M-C, Yang SF (2001) Signaling events in the hypoxic induction of alcohol dehydrogenase gene in *Arabidopsis*. Plant Physiol 126:742–749

Pien S, Wyrzykowska J, McQueen-Mason S, Smart C, Fleming A (2001) Local expression of expansin induces the entire process of leaf development and modifies leaf shape. Proc Natl Acad Sci USA 98:11812–11817

Raskin I, Kende H (1983) How does deepwater rice solve its aeration problem. Plant Physiol 72:447–454

Raskin I, Kende H (1984) Regulation of growth in stem sections of deep-water rice. Planta 160:66–72

Rohila JS, Yang Y (2007) Rice mitogen-activated protein kinase gene family and its role in biotic and abiotic stress response. J Integr Plant Biol 49:751–759

Saika H, Okamoto M, Miyoshi K, Kushiro T, Shinoda S, Jikumaru Y, Fujimoto M, Arikawa T, Takahashi H, Ando M, Arimura S, Miyao A, Hirochika H, Kamiya Y, Tsutsumi N, Nambara E, Nakazono M (2007) Ethylene promotes submergence-induced expression of *OsABA8ox1*, a gene that encodes ABA8′-hydroxylase in rice. Plant Cell Physiol 48:287–298

Santner A, Calderon-Villalobos LIA, Estelle M (2009) Plant hormones are versatile chemical regulators of plant growth. Nature Chem Biol 5:301–307

Stünzi JT, Kende H (1989) Gas composition in the internal air spaces of deepwater rice in relation to growth induced by submergence. Plant Cell Physiol 30:49–56

Voesenek LACJ, Benschop JJ, Bou J, Cox MCH, Groenveld HW, Millenaar FF, Vreeburg RAM, Peeters AJM (2003) Interactions between plant hormones regulate submergence-induced shoot elongation in the flooding-tolerant dicot *Rumex palustris*. Ann Bot 91:205–211

Vriezen WH, Hulzink R, Mariani C, Voesenek LACJ (1999) 1-Aminocyclopropane-1-carboxylate oxidase activity limits ethylene biosynthesis in *Rumex palustris* during submergence. Plant Physiol 121:189–196

Xiong L, Zhu JK (2003) Regulation of abscisic acid biosynthesis. Plant Physiol 133:29–36

Xu K, Xu X, Fukao T, Canlas P, Maghirang-Rodriguez R, Heuer S, Ismail AM, Bailey-Serres J, Ronald PC, Mackill DJ (2006) Sub1A is an ethylene-response-factor-like gene that confers submergence tolerance to rice. Nature 442:705–708

Yang SH, Choi D (2006) Characterization of genes encoding ABA 8′-hydroxylase in ethylene-induced stem growth of deepwater rice (*Oryza sativa* L.). Biochem Biophys Res Commun 350:685–690

Zarembinski TI, Theologis A (1993) Anaerobiosis and plant growth hormones induce two genes encoding 1-aminocyclopropane-1-carboxylate synthase in rice (*Oryza sativa* L.). Mol Biol Cell 4:363–373

Zarembinski TI, Theologis A (1997) Expression characteristics of OS-ACS1 and OS-ACS2, two members of the 1-aminocyclopropane-1-carboxylate synthase gene family in rice (*Oryza sativa* L. cv. Habiganj Aman II) during partial submergence. Plant Mol Biol 33:71–77