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Survival strategies adopted by plants during flooding

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Abstract
Water is essential for plant growth and development but excessive water adversely affects plant fitness in natural and agricultural ecosystems. This results in restricted gas exchange, low light levels under water and formation of potentially toxic compounds that leads to carbon and energy crisis. Plant respond to it through various submergence survival strategies involving ethylene and gibberellin driven module that control the growth of submerged plant parts. Evidences from genetic and molecular studies suggests that plant tolerance to flooding is commonly governed by key regulatory components encoding transcription factors, protein kinases and upstream components as a result of altered homeostasis in oxygen, ethylene and energy reserves. Further mechanistic understanding of survival strategies at physiological and molecular levels can contribute to identify the potential regulatory network governing survival under flooding to stabilize crop yields in flood prone environments.

Keywords: Flooding, submergence, aerenchyma, anoxia, waterlogging

Introduction
Global flood risk under climate change has increased dramatically in recent years that negatively affected terrestrial plant life. Floods adversely affects agricultural yields by delaying planting time, reducing vigor and increased susceptibility to pests and diseases. Going by the scientific reports of IPCC, frequency of floods is projected to increase in Southeast Asia, East Africa and northern parts of South America this century. Excess of soil water decreases the oxygen diffusion rate into the soil because of the 10^4 lower diffusion of gases into water with respect to air. Soon after the soil is flooded, root respiration and micro-organisms drains the leftover oxygen and the soil environment becomes hypoxic (*i.e.* reduced oxygen levels limit mitochondrial respiration) and later on anoxic (*i.e.* respiration is inhibited completely). So, the first limitation for plant growth is the immediate lack of oxygen which is neccessary to sustain aerobic respiration of submerged plant tissues. Also, there is a restricted outward diffusion of ethylene. As flooding duration increases, another problem associated with excess of soil water appears as a result of the progressive decrease in the soil reduction-oxidation potential that leads to the formation of potentially toxic compounds such as sulfides, soluble Fe and Mn, lactic acid, ethanol, acetaldehyde, acetic acid and formic acid. Therefore, the lack of oxygen and later the accumulation toxic compounds hampers plant growth under flooding conditions. Although prolonged flooding considerably affects their productivity and viability, plants are equipped with various survival mechanisms to cope with a transient influx of water into their environment. Flood-tolerant plants are characterized by a continuum of survival strategies that include low oxygen escape syndrome (LOES) and low oxygen quiescence syndrome (LOQS). Low oxygen escape strategy (LOES) involves shoot elongation by internode and petiole elongation upon submergence and further shoot elongation with increasing water depth. Traits of escape phenotypes include enhanced shoot elongation, hyponasty (upward bending of leaves), aerenchyma formation, induction of barrier to radial oxygen loss (ROL) in roots, adventitious root formation, gas film formation on the leaf surface and modification of leaf anatomy. Contrary to the energy-consuming LOES, LOQS manages metabolism and limits growth. It is associated with plants that endure prolonged complete submergence. To maintain cellular homeostasis under lack of oxygen, starch catabolism, glycolysis, ethanolic fermentation and a bifurcated tricarboxylic acid (TCA) cycle are used to fuel substrate-level ATP production and support the synthesis of proteins involved in metabolite transport, chaperone activity and ROS scavenging. This is accompanied by decrease in energy consuming processes associated with cell division and growth, including DNA, protein, ribosome and cell wall synthesis.

Root acclimation to waterlogging

Oxygen concentration that can be maintained in the root tip meristem is determined by three factors: rate of respiration, internal oxygen diffusion (determined by the tissue porosity, the tortuosity of the longitudinally connected air channels, and diffusion path length) and outward diffusion of oxygen to the environment (i.e. radial oxygen loss (ROL). Key responses to increase ventilation involves aerenchyma or adventitious roots formation and reduced oxygen loss by barrier formation. Aerenchyma is constitutively present or inducible upon flooding that facilitate the inward diffusion of oxygen in roots and outward diffusion ethylene generated by roots and methane generated under anaerobic conditions in soil. It develops in the existing shoot or root tissues secondary tissues or adventitious roots. It is formed by separation of previously connected cells (schizogenous aerenchyma), programmed cell death (PCD) in the root cortex (lysigenous aerenchyma), or cell division and cell expansion without separation or lysis (expansigenous aerenchyma). Aerenchyma formation requires ethylene, secondary messenger Ca^{2+} and ROS signaling and finally cell wall degradation. Aerenchyma formation in deep water rice stem is associated with an elevation in ROS and down-regulation of METALLOTHIONEIN 2b mRNA. ROS is probably generated by the Ca2+-dependent plasma membrane-localized respiratory burst oxidase homologs (RBOHs) that promote apoplastic superoxide production to amplify ROS-mediated signaling that triggers PCD of cortical cells. Thus, aerenchyma promotes relatively high concentration of oxygen in roots. However, this oxygen can be lost by outward diffusion into the soil i.e. radial oxygen loss (ROL). It can be prevented by constitutive or inducible apoplastic barrier composed of suberin that is formed in the exodermal/hypodermal space present near the root tip and lignified schlerenchyma/epidermal cells. This serves as an effective ROL barrier and blockade between living root cells and outside anaerobic and toxic environment. Malic acid serves as a substrate for fatty acid biosynthesis and thus a precursor for the formation of suberin. Molecular investigations reveals involvement of ATP binding cassette(ABC) transporter (RCN1/OsABCG5) in the export of very long chain fatty acids and/or their derivatives across the hypodermal plasma membrane into the apoplast where they serve as major components of suberin. Another response includes adventitious root formation from submerged stem nodes mediated by ethylene. It involves localized degeneration of epidermal cells driven by localized force of the emerging root meristem.

Low oxygen escape syndrome (LOES)

Some plants in flood prone environment has the ability to elongate shoots when underwater because shoot to root aeration is far more efficient than internal aeration of roots via aerenchyma formation, underwater photosynthesis by mesophyll cells or influx of oxygen from water layers into shoots. But this trait is restricted to limited number of species because of higher carbon cost. In species examined to date, it involves ABA as a repressor and GA/auxin as promoter of underwater elongation growth of submerged stems and leaves. The LOES of 'deepwater' rice involves two ERF-VII TFs SK1, SK2 and two additional uncharacterized loci on chromosomes 1 and 3. The ethylene-triggered induction of SK1/2 during submergence leads to up-regulation of mRNA encoding a rate-limiting GA20 oxidase (GA20ox), which correlates with increased concentrations of bioactive GA1 and GA4 in internode tissue, further promoting stem elongation.

Low oxygen quiescence strategy (LOQS)

Plant remains in quiescence state upon submergence and resumes growth once the flood water receeds. It is GA mediated and operates in Scuba rice. It is energy conserving strategy and operates under complete submergence. SUB1 (Submergence 1) locus involved in this strategy was identified in the submergence tolerant FR13A landrace from Orissa. The locus encodes two to three transcription factors belonging to group VII of ERF family. All rice accessions surveyed so far contains SUB1B and SUB1C genes at the SUB1 locus, whereas SUB1A was restricted to some indica and aus varieties. Constitutive and conditional expression of SUB1A conferred survival of complete submergence for 14–16 days. Submergence promotes biosynthesis and prevent outward diffusion of ethylene, which stimulates mRNA accumulation of SUB1A. However, SUB1A eventually limits ethylene production, leading to the reduction of ethylene-mediated gibberellic acids (GA) production. SUB1A also increases the content of brassinosteroids, which augments degradation of bioactive GA. Increased BR content contributes to the accumulation of SLENDER RICE1 (SLR1), a DELLA protein that negatively regulates GA signaling. Positive feedback regulation of SUB1A and BR can further boost SUB1A-dependent hormonal regulation, resulting in the limited GA-mediated elongation growth. Therefore, SUB1A mediated tolerance involves reduction of usage of stem carbohydrates and thus preventing energy crisis later on.

Conclusions and future perspectives

Carbon and energy crisis poses a serious threat to plant survival under flooded condition. Evidences from genetic and molecular studies suggests that plant tolerance to flooding is commonly governed by key regulatory components encoding transcription factors, protein kinases and upstream components as a result of altered homeostasis in oxygen, ethylene and energy reserves. A 'learn from nature' approach has to be adopted to identify and tansfer genes present only in species adapted to flooding. Coupling physiological studies with advance genomic technologies provides an excellent opportunity to provide insurance against unanticipated flooding and improve crop yields.

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