Waterlogging and submergence stress: affects and acclimation

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Abstract

Submergence, whether partial or complete, imparts some serious consequences on plants grown in flood prone ecosystems. Some plants can endure these conditions by embracing various survival strategies, including morphological adaptations and physiological adjustments. This review summarizes recent progress made in understanding of the stress and the acclimation responses of plants under waterlogged or submerged conditions. Waterlogging and submergence are often associated with hypoxia development, which may trigger various morphological traits and cellular acclimation responses. Ethylene, abscisic acid, gibberellin and other hormones play a crucial role in the survival process which is controlled genetically. Effects at the cellular level, including ATP management, starch metabolism, elemental toxicity, role of transporters and redox status have been explained. Transcriptional and hormonal interplay during this stress may provide some key aspects in understanding waterlogging and submergence tolerance. The level and degree of tolerance may vary depending on species or climatic variations which need to be studied for a proper understanding of waterlogging stress at the global level. The exploration of regulatory pathways and interplay in model organisms such as Arabidopsis and rice would provide valuable resources for improvement of economically and agriculturally important plants in waterlogging affected areas.

Introduction: Plant’s association with waterlogging and submergence

Growth and development of plants are severely influenced by stagnant waterlogged or submerged conditions. Plants grow on arable farmland or a watery environment show differential responses to the stress. The level of variation in response to excess water stress is a critical issue regulating abundance and distribution of plants (Blom & Voesenek, 1996). The differential survival property and the degree of tolerance observed in closely related plants belonging to the same genus is a key aspect of waterlogging and/or submergence tolerance. Rice (Oryza sativa L.) is particularly tolerant to submergence, whereas tomato (Solanum lycopersicon L.) is highly intolerant (Ahsan et al., 2007). Within species, Mentha arvensis is more tolerant towards waterlogging than Mentha piperita (Phukan et al., 2014). Variation in waterlogging tolerance has also been observed in Echinodorus varieties (Fukao et al., 2003), mangroves (Cheng et al., 2015a,b) and legume sp. [Pisum genotypes, lentil genotypes and Lathyrus (Malik et al. 2015)]. Gibberd et al. (2001) measured waterlogging tolerance among a diverse range of Trifolium accessions which differ in root porosity, lateral root formation and “aerotropic rooting”.

Whether genus or species, approximately 16% of the fertile areas of the world are affected by soil waterlogging and the average yield loss due to spring floods or excess rainfall is estimated to be 40–80%, which can vary depending on the stage of plant development (Ahsan et al., 2007; Setter et al., 1999; Shaw et al., 2013). The estimated annual damage from crop loss is estimated to be in excess of billions of dollars, which empathizes the need to take waterlogging stress very seriously (Voesenek and Bailey-Serres, 2013; Pucciariello et al., 2014; Voesenek & Sasidharan, 2013).

The exact mechanism that affects growth and development of plants under excess water is unclear because water is chemically harmless, but certain physical properties of water, most notably its ability to interfere with the free gas exchange, can injure and kill plants (Vartepetian & Jackson, 1997). During submergence, plants are partially or completely covered with water, which limits light intensity, gas diffusion and effusion of soil nutrients. This may lead to morphological damage and increased susceptibility to pests and diseases (Catling, 1992; Greenway & Setter, 1996). Partial submergence, often referred to as waterlogging, leads to reduced gas diffusion, growth of microorganisms and production of toxic substances such as Fe2+, Mn2+ and H2S (Huang et al., 2015; Setter et al., 2009). Whether it is partial and/or fully submerged conditions, there occurs a limited supply of O2 a condition generally called hypoxia. If waterlogging persists for a prolonged period, it confers enhanced hypoxic stress and is thought to impose a variety of adverse effects on plants.
which can upset plant physiology and normal metabolism. Along with O₂, other gases like CO₂ and ethylene also diffuse slowly in water (Gibbs & Greenway, 2003). Soil chemistry also alters due to reduced gas movement and because of the growth of microorganisms which leads to accumulation of soluble organic and inorganic substances. To avoid these unfavorable conditions, endogenous accumulation of ethylene in tissues surrounded by water activates adaptive signal transduction pathways. In these pathways, ethylene production is perceived by ETR1 (ethylene-binding receptors), which activates EIN2/EIN3 (ethylene insensitive) and leads to expression of ethylene response factor (ERFs) transcription factors in the nucleus (Pierik et al., 2006).

Recent transcriptome and/or microarray data of Arabidopsis (Hsu et al., 2011; Licausi et al., 2011), maize (Thirunavukkarasu et al., 2013), cotton (Christianson et al., 2010), soybean (Tamang et al., 2014), Jatropha (Juntawong et al., 2014), Taxodium (Qi et al., 2014) has provided a diverse set of transcripts operating during the stress. It provides a deeper understanding of the molecular mechanisms occurring when plants are confronted with waterlogging stress followed by hypoxia. Evaluating the response of excess water stress on a global scale depending on the climate, genus and evolution provides an ideal opportunity to investigate the inter- and intra-specific variation in waterlogging tolerance in the whole ecosystem. Fundamental insight into transcriptional regulation, downstream signal transduction, biochemical and physiological alterations that promotes waterlogging and submergence tolerance could provide the key for increased crop production under these adverse environmental conditions. In this review article, we summarize the current understanding of the consequences and acclimation responses of plants associated with waterlogging or submergence stress.

Morphological and anatomical alterations

To escape the hypoxic environment or at least improve oxygen diffusion to the submerged organs, plants undergo different morphological adaptations like epinasty, reduction in the size of the stomatal aperture, hypostomatic growth, shoot elongation, leaf acclimations, suberized exodermis, hypertrophy of lenticels, aerenchyma formation and adventitious root development (Bailey-Serres & Voesenek, 2008; Voesenek & Bailey-Serres, 2015). These adaptations are considered in greater detail as follows.

1. Downward movement (epinasty) of leaf petioles occurs due to hypoxia and are observed in relatively sensitive species like Lycopersicon esculentum (Jackson & Campbell, 1976) and Quercus petraea (Parelle et al., 2007). Stomatal closure in Arabidopsis thaliana in response to waterlogging primarily prevents excessive transpiration to maintain leaf water potential, which further delay leaf senescence and chlorosis (Liu et al., 2012). Petiole elongation and hyponasty in Rumex palustris (Cox et al., 2004) and Arabidopsis (Rauf et al., 2013) allows the plant to evade the water surface and restore gaseous exchange. Closely related R. palustris and R. acetosa show inhibition and stimulation of petiole elongation, respectively, upon submergence (Rijnders et al., 1997). To facilitate gaseous movements in submerged or waterlogged plants, the phenomenon of formation of leaf gas films occur which permit exchange of CO₂ and O₂ between the leaves and surrounding waters. It results from the trapped air that enlarges the water–gas interface on the hydrophobic surfaces of leaves when submerged (Pedersen et al., 2009). Their role in providing submergence tolerance has been observed in rice, S. anglica and other wetland species (Colmer & Pedersen, 2008; Pedersen et al., 2009).

Leaf gas film helps in maintaining the underwater net photosynthesis rate and pO₂ (O₂ partial pressure) level by CO₂ uptake when there is sufficient light while it maintains the pO₂ level by O₂ uptake when there is no light (Colmer & Pedersen, 2008).

2. Rapid shoot elongation as seen in Mentha arvensis (Phukan et al., 2014) is another escape mechanism adapted by plants to resist and survive waterlogging stress. The submergence 1A (SUB1A), is an ERF that confers submergence tolerance via limiting shoot elongation and GA signaling (Pena-Casto et al., 2011). The submergence tolerant FR13A variety of rice having SUB1A does not elongate upon submergence, but re-grows after de-submergence while some Indica and Japonica varieties lacking SUB1A rapidly elongate under submergence to escape the stress (Kudahettige et al., 2010; Xu et al., 2006).

Hypertrophied lenticels appear as swelling of tissues at the stem base and are believed to result from radial cell division and expansion as shown in Glycine max (Shimamura et al., 2010). They are observed in many gymnosperms [Abies balsamea (Hahn et al., 1920), Araucaria bidwilei (Hahn et al., 1920), Larix laricina (Hahn et al., 1920), Picea sp. (Islam et al., 2003), Pinus sp. (Topa & McLeod 1986) and Taxus sp. (Hahn et al., 1920)] and angiosperms [Distylium chinense (Liu et al., 2014), Soybean (Shimamura et al., 2010), Hevea brasiliensis (Sena Gomes & Kozlowski, 1988), Pyrus sp. (Andersen et al., 1984b), Ulmus americana (Newsome et al., 1982)] during flooding. It is associated with auxin and ethylene production. It facilitates downward diffusion of O₂ as well as potential venting of compounds produced in the roots as byproducts of anaerobic metabolism like ethanol, CH₄ and CO₂ (Kozlowski, 1997).

Leaf acclimations under submergence include 20% thinning and increased specific leaf area (SLA) like in R. palustris (Mommer et al., 2006). Leaves also acclimates itself by thinner epidermal cell walls and cuticles, also by lying chloroplast closer to the epidermis, which helps CO₂ enter mesophyll cells by diffusion rather than stomata (Mommer et al., 2005).

3. Development of the suberized exodermis on the periphery of the cortex acts as a barrier to prevent radial oxygen loss (ROL) as seen in the roots of rice (Kotula et al., 2009; Kulichikhin et al., 2014). This also protects the plant from phytotoxins produced by microorganisms in the environment surrounding the roots (Soukup et al., 2007). Suberized exodermis development correlates with the formation of aerenchyma in maize (Enstone & Peterson, 2005). Plant species whether flood tolerant or intolerant tends to form these lacunae gas spaces (aerenchyma) and the proportion of this aerenchyma is generally considered to be a key factor when discriminating wetland and non-wetland plants (Vasellati et al., 2001). Garthwaite et al. (2003) showed diversity in root aeration traits associated with waterlogging tolerance in the genus Hordeum with 35 wild Hordeum accessions. An increase in porosity enhances venting of
phytotoxic compounds (ethanol, methane) formed in roots towards the shoot and finally to the atmosphere (Visser & Pierik, 2007; Yin et al., 2013). It also enhances the longitudinal diffusion of gases in roots under hypoxia (Xu et al., 2013). Aerenchyma is also observed in leaf sheaths following waterlogging favoring shoot-root ventilation (Fabbri et al., 2005). Sometimes, aerenchyma are connected to the stomata which allow gaseous flow from leaves to the basal part of the plants as seen in the mature leaf sheaths of rice (Matsukura et al., 2000). Also, it is interrupted by septa of stellate cells carrying large intercellular spaces to facilitate O₂ exchange (Hoshikawa, 1989). The active cell death process which takes place during aerenchyma development is genetically controlled (Buckner et al., 2000). In the case of Sagittaria lancifolia nuclear changes (clumping of chromatin, fragmentation and disruption of nuclear membrane) are the earliest events followed after flooding. This is followed by plasma membrane crenulation, tonoplast disintegration, organelle swelling and disruption, loss of cytoplasmic contents, collapse of the cell and finally leads to aerenchyma formation (Schussler & Longstreth, 2000). Evans (2004) described that aerenchyma is formed either by schizogyen in which development results in cell separation or lysogeny in which cell death results in formation of gas spaces. Ethylene, whether endogenously produced or exogenously applied, is mainly responsible for aerenchyma formation through lysogeny in which it signals ROS production, thereby leading to cell death. Another probable mechanism described by Shabala (2011) is that the decrease in cytosolic K⁺ pool leads to activation of caspase-like proteases which are key enzymes involved in apoptotic cascade. H⁺-coupled movement of undissociated phenolic acid across the plasma membrane or increases in the cytosolic free Ca²⁺ pool results in a decrease in the concentration of cytosolic K⁺ pool (Demidchik et al., 2010; Shabala et al., 2007). This leads to PCD and the formation of aerenchyma. Ethylene independent aerenchyma formation is also observed in a submergence tolerant variety of rice like FR13A. This variety of rice adapts the LOQS strategy and does not show any increase in ethylene production when submerged. ROS accumulation plays the central role in aerenchyma formation in FR13A while in the fast-longating Arborio Precoce variety ethylene plays the central role (Parlanti et al., 2011). In addition, nutrient deprivation also leads to formation of gaseous spaces as seen in maize root cortex in which starvation of N or P greatly enhances the sensitivity of ethylene-responsive cells leading to cell lysis and aerenchyma formation (He et al., 1992).

4. As waterlogging proceeds, the decaying basal roots become incapable of supplying required water and minerals to the plant (Gibberd et al., 2001). Consequently, formation of adventitious roots (AR) becomes an adaptive response in many plants like tomato (Vidoz et al., 2010), Rumex (Visser et al., 1996), sunflower, sugarcane (Jackson, 1955) and Mentha (Phukan et al., 2014) which functionally replaces the basal roots. Along with it, many gymnosperms (Picea sitchensis, Pinus contorta, Sequoia sempervirens, Tamarix gallica, Taxodium distichum and Thuja plicata) and angiosperms (Populus deltoides, Quercus robur, Eucalyptus camaldulensis, Hevea brasiliensis, Malus domestica, Cydonia oblonga and Salix atrocinerea) develop ARs during flooded conditions (Andersen et al., 1984a; Argus et al., 2015; Kozlowski, 1997). ARs are commonly formed near the base of the stem or in the region where lenticels are abundant, and their growth is lateral, parallel to the water-soil surface. They emerge at the interface between the water saturated soil and atmosphere reflecting their importance in replacing the normal root system, both underwater and following retreat of the water table. The ability to produce these adventitious roots is commonly associated with ethylene production (Abiko et al., 2012; Steffens et al., 2006) which increases auxin sensitivity in Rumex (Visser et al., 1996) promoting cell-wall loosening. It reduces the mechanical resistance of stem tissues to facilitate new root emergence. In deepwater rice, ethylene facilitates the emergence of pre-formed ARs by causing death of the epidermal cells that cover the root tip (Mergemann & Sauter, 2000). One important attribute associated with ARs is the development of a barrier to ROL, a zone in the external cell layers in the sub-apical region that shows very low radial permeability to O₂ (Colmer, 2003a). Barrier to ROL along with aerenchyma enhances longitudinal O₂ diffusion towards the hypoxic tissues. Certain wetland species like Juncus effuses, Schoenoplectus validus, Phragmites australis and Glyceria maxima retain the barrier to ROL constitutively while in some species like rice, wild Hordeum Rumex crispus and Cyperus eragrostis, it is inducible under hypoxic environment (Colmer, 2003b; Garthwaite et al., 2003; Manzur et al., 2014; McDonald et al., 2002; Soukup et al. 2007; Visser et al., 2000). On the other hand, barley and wheat do not form any barrier to ROL (McDonald et al., 2001). The strength of the barrier can be variable which could be evaluated by the O₂ flux from the basal regions of adventitious roots (Colmer, 2003b). Radial O₂ permeability across the exterior of the roots through the barrier also declines because of the respiratory consumption in the outer cell layers and secondary wall deposition in them (Armstrong et al., 2000; Soukup et al., 2007). Detoxification by major elemental phytotoxins is also influenced by a barrier to ROL because it prevents oxidation of the rhizosphere due to increased ROL.

Figure 1 illustrates the morphological and anatomical adaptations adapted by plants under waterlogging and submergence stress.

Effects at the cellular level

1. Under waterlogged condition O₂ level falls below 20.9% causing hypoxia condition. In 1 day of flooding, O₂ partial pressure may declines from 20.9 to 1 kPa depending on a variety of variables including temperature, soil, soil organic content and microbial activity (Nilsen & Orcutt, 1997). For self-repair, maintenance and sustaining tissue or organ specific functions cells require mitochondrial oxidative phosphorylation of ATP. That process consumes O₂ in proportion to the rate of ATP utilization by the cells. Therefore, O₂ depletion in waterlogged or submerged conditions lends rapid and profound consequences on cell physiology. To survive this energy crisis, ATP consuming processes such as DNA synthesis and cell division are curtailed (Gibbs & Greenway, 2003). Anaerobic generation of ATP from glycolysis and fermentation of pyruvate to ethanol (catalyzed by PDC, ADH) or lactate (catalyzed by LDH) yielding NAD⁺ are the major events to sustain anaerobic
carbon metabolism (Albrecht et al., 2004). In some plants like maize, there Arabidopsis occurs a rapid spike in cytosolic Ca^{2+} under hypoxia, which ultimately alters the expression of hypoxia responsive genes (Bailey-Serres & Chang, 2005; Subbaiah & Sachs, 2003). Other acclimation responses include management of level of metabolites like fructose, pyruvate, sucrose, increased biosynthesis of alanine, γ-aminobutyric acid (GABA), succinate and occasionally malate (Bailey-Serres & Voesenek, 2008; Gibbs & Greenway, 2003). For fructose-1,6-bis-P synthesis, fructose 6-phosphate dikinase (PFK) is used instead of phosphofructokinase (PFK) and for pyruvate synthesis, pyruvate phosphate dikinase (PPDK) is used instead of pyruvate kinase (PK). UDP-dependent sucrose synthase (SUS) is used instead of invertase for sucrose catabolism and PPI-dependent enzymes are preferred to ATP-dependent enzymes (Liu et al., 2005; Narsai et al., 2009). Hypoxia leads to ROS production and in turn ROS mediated signaling promotes various defense responses, programmed cell death, and developments in plants like in rice (Steffens & Sauter, 2009; Steffens et al., 2012) and wheat (Cheng et al., 2015a,b). H_{2}O_{2} mediates emergence of adventitious roots and promotes lysigenous aerenchyma formation in internodes of rice stems (Steffens et al., 2011). In Arabidopsis, ROS originating in mitochondria activate the mitogen-activated protein kinase MAPK6 to improve survival at hypoxic conditions (Chang et al., 2012). However, excess ROS brings on oxidative damage to cells (oxidize proteins, lipids and nucleic acids) which is checked by enzymes like SOD, CAT, APX, POD GPX and MDHAR (Arbona et al., 2008; Sharma et al., 2012). ROS defense and signaling cascades are tightly regulated in plants to maintain a proper balance between survival and stress tolerance (Luo et al., 2012). Limited O_{2} and ATP supply affects cell survival beyond few hours of hypoxia unless the available amount of energy is redirected to regulate anaerobic metabolism, pH maintenance and ROS detoxification.

2. Two versus 38 ATP molecules in anaerobic mode would prefer greater carbohydrate content in roots and an efficient mechanism for carbohydrate mobilization so that the cell could survive prolonged oxygen deprivation (Das et al., 2005). When Panda & Sarkar (2014) studied six Indica rice [Oryza sativa (L.)] cv for non-structural carbohydrate (NSC) accumulation, tolerant cultivars (FR 13A, Kalapatutia, Khoda and Khadara) accumulated greater contents of NSC compared to the susceptible cultivars (Sarala and IR 42). Tolerant pigeon pea (Cajanus cajan L.) genotypes ICPL 84023 and ICP 301 showed higher total, reducing and non-reducing sugar content than ICP 7035 and Pusa 207 (Kumutha et al., 2008). The flooding escape strategy also determines carbohydrate levels (Kudahettige et al., 2010). It either does not elongate shoots, conserve energy and carbohydrate consumption and later on re-grows after desubmergence (low oxygen quiescene syndrome – LOQS) as stated above or rapidly extends their shoots and leaf blades to reach the water surface for re-establishing gas exchange (low oxygen escape syndrome – LOES) (Bailey-Serres & Voesenek, 2008). Mentha arvensis showed tolerance towards waterlogging by consuming carbohydrate levels and rapidly elongating while Mentha piperita showed susceptibility, though it was conserving its carbohydrate reserve (Phukan et al., 2014). Starch mobilization also plays a major role in sustaining excess water stress as seen in some Echinochloa species (Fukao et al., 2003), Potamogeton pectinatus tubers (Dixon et al., 2006), mung bean (Sairam et al. 2009), cotton (Kuai et al., 2014) and Cynodon dactylon (Li et al., 2015).

3. Plasma and organelle membrane transporters play an important role in waterlogging tolerance (Shabala et al., 2014). One of them is an H^{+}-ATPase pump which consumes ATP for secondary active transport. Under hypoxia, the ATP content decreases and as a result H^{+}-ATPase activity decreases in soybean and sunflower roots which impairs ion transport processes (Mukherjee et al., 1986; Shen et al., 2006). Also, inhibition of H^{+}-ATPase and ferric-chelate reductase leads to Fe deficiency in waterlogged citrus (Martinez-Cuenca et al., 2015). Uptake of essential cations like K^{+}, NH_{4}^{+} and Mg^{2+} is thus reduced as well as uptake of essential anions like PO_{4}^{2-}, NO_{3}^{-} or SO_{4}^{2-} through H^{+} symport system (Kreuzwieser & Gessler, 2010; Marschner, 1995;
Hypoxia stress following waterlogging assists soil micro-plant growth and development (Melhuish et al., 1991). Soil redox potential. Denitrification of both inorganic and organic substances like ethanol, acetaldehyde and various short-chain fatty acids and phenolics either produced in plants or rhizosphere microorganisms (Armstrong & Armstrong, 1999; Drew & Lynch, 1980). Even micromolar concentrations of phenolic acid in waterlogged soil can inhibit root growth of rice (Tanaka et al., 1990). During waterlogging stress due to slower gas exchange, high $pCO_2$ develops in the root zone which leads to higher concentration of $HCO_3^-$ in the cytoplasm. Some wetland species like rice can tolerate this condition while it imparts some severe effects on root growth and metabolism in non-wetland species (Greenway et al., 2006). Similarly, under higher concentration of $Fe^{2+}$, rhizosphere pH and $HCO_3^-$ in flooded soils decrease. Then $Fe^{2+}$ is accompanied inside cells with non-volatile anions like $Cl^-$ or $SO_4^{2-}$ and oxidation of $Fe^{2+}$ leads to cytoplasmic acidification as well as impairment of cell metabolism (Shabala, 2011). Due to the increased microbial action, ethylene, which helps in various adaptive responses during waterlogging, can also accumulate to phytotoxic concentrations and can influence physiological responses at the cellular or the whole plant level. It is shown that nitrate uptake by tomato plants increased under prolonged periods of root hypoxia, which basically limits the effect of diminishing $O_2$ content (Horchani et al., 2010; Morard et al., 2004). This is probably due to the nitrate reductase (NR) activity which promotes $NAD^+$ generation as species tolerant to oxygen deprivation exhibit higher NR activity than sensitive ones (Bailey-Serres & Voesenek, 2008; Limami et al., 2014). It has been shown that the absence or the decrease in NR activity enhances the symptoms of hypoxia (Stoimenova et al., 2003). Along with nitrate, nitrite concentration also increases in hypoxic tissues and is preferentially used for NO synthesis (Oliveira & Sodek, 2013). NO acts as a signal molecule involved in different physiological processes and adaptive responses to abiotic stresses including waterlogging (Besson-Bard et al., 2008a,b).

**Transcriptional and hormonal interplay during hypoxia stress**

1. Crosstalk and interplay of different phytohormones like ethylene, ABA and GA play an important role in submergence and waterlogging tolerance. Due to biosynthesis and physical entrapment, the level of ethylene increases in waterlogged plants and it has been identified as the signal for the regulation of the early response to flooding (Voesenek et al., 2013). The programmed cell death response that results in lysigenous aerenchyma formation is also controlled by ethylene (Yamauchi et al., 2014), as is epidermal cell death above adventitious root primordial in rice (Mergemann & Sauter, 2000) and adventitious root growth in *Rumex palustris* (Visser et al., 1996) rice (Steffens & Sauter, 2005) and tomato (Vidziol et al., 2010). Plants with slow root ethylene synthesis (e.g. rice) show a positive response to ethylene which decreases the level of ABA, enhances tissue sensitivity to GA and stimulates growth of submerged internodes (Knaap et al. 1996). Resistance of *Rumex palustris* plants to flooding is a consequence of rapid shoot elongation promoted by ethylene (Herzog & Pedersen, 2014). Ethylene also plays a role in other differential growth processes like petiole epinasty (Parelle et al., 2013), shoot gravitropism (Friedman et al., 2003), seedling apical hook (An et al., 2012) and shading induced hyponasty (Polko et al., 2013; Vandenbussche et al., 2003). Ethylene regulates activation of genes involved in better survival and escape during hypoxia.
stress (van Veen et al., 2014). Group VII ERFs from Arabidopsis (RAP2.2, HRE1 and HRE2) and rice (Sub1A, SK1, SK2) play important roles in providing hypoxia tolerance (Fukao et al., 2006; Hattori et al., 2009; Hinz et al., 2010; Licausi et al., 2010). These group VII ERFs from Arabidopsis are regulated by N-end rule pathway in which ATE1/2 and PRT6 recognizes N-terminal Met Cys motif and leads to its ubiquitination under normal conditions (Kosmacz et al., 2015; Licausi et al., 2013). Similarly, ERF1 from barley is a substrate of N-end rule pathway (Mendiondo et al., 2015). Though Sub1A also possesses the N-terminal motif it is not a target of N-end rule mediated degradation (Gibbs et al., 2011). Ethylene and hypoxia responsive RAP2.2 (Homologue of Sub1A) promotes upregulation of genes involving fermentation pathway enzymes (ADH1, PDC1 and LDH1), sugar metabolism (SUS1 and SUS4) and ethylene biosynthesis (ACS7 and ACO1) in Arabidopsis (Hinz et al., 2010). HRE1 and HRE2 also show Hypoxia and ethylene response, upregulating ADH1, PDC1 and SUS but unlike RAP2.2 they inhibit ethylene signaling and promote GA response. One of the highly induced genes in submergence is WRKY22 which provides hypoxia tolerance by directly binding to ACS7 promoter and activating downstream ethylene signaling (Hsu et al., 2013). Rice homologues Sub1A and Sub1C are induced by ethylene but acts antagonistically to each other in response to submergence. Sub1C is inhibited by Sub1A and acts through CIPK15 (Calcineurin B-like interacting protein kinase 15) and RAMY3D pathway. Intolerant varieties lacking Sub1A display ethylene-mediated ABA degradation, GA responsiveness and fast elongation under flooding under Sub1C regulation (Fukao & Bailey-Serres, 2008; Kudahettige et al., 2010; Pena-Castro et al., 2011). Some wild-type rice genotypes (O. rhizomatis and O. eichingeri belonging to C-genome group) lacking SUB1A also show reduced growth and submergence tolerance indicating a SUB1A-independent tolerance mechanism (Niroula et al., 2012). Ethylene also mediates upregulation of EIN3 (involved in ethylene biosynthesis) which directly binds to SNORKEL1 (SK1) and SNORKEL2 that triggers considerable internode elongation via ethylene and GA (Hattori et al., 2009; Nagai et al., 2010). Figure 2 illustrates the possible pathway and interplay of hypoxia responsive genes and hormones involved during submergence or waterlogging stress.

Figure 2. Transcriptional and hormonal regulation during waterlogging and submergence stress. The figure depicts the interplay and crosstalk of different hormones and transcripts that affects tolerance and susceptibility of Arabidopsis and rice during submergence and waterlogging. In Arabidopsis transcription factors like ERF and WRKY counteracts the effects produced by hypoxia like senescence, ROS generation and reduced water loss to resist hypoxia response. While in rice SK1/SUB1A adapts escape or quiescence strategy to survive hypoxia.

2. Phytohormones ABA and GA influence the leaf orientation in different ways. GA induces leaf hyponasty of Pittosporum eugenioides, whereas ABA induces epinasty (Dwyer et al., 1995). Endogenous ABA concentration does not decrease upon flooding in soybean, though its content decreases in untreated plant. Also, exogenous application of ABA on soybean showed a better transcriptional response, suggesting the involvement of ABA in the enhancement of flooding tolerance (Komatsu et al., 2013). Waterlogging also induces ABA accumulation and in turn both induce ethylene response factor RAP2.6 that leads to increased ROS and antioxidant defense in Arabidopsis (Liu et al., 2012). ABA causes an increased generation of $\mathrm{O}_2^-$ and $\mathrm{H}_2\mathrm{O}_2$ (Jannat et al., 2011), promotes stomatal closure and stress-related gene expression (Rodríguez-Gamir et al., 2011). In contrast, certain species like Rumex (Benschop et al., 2005), certain rice varieties like AP shows ethylene-mediated ABA degradation during submergence which promote GA mediated elongation response (Fukao & Bailey-Serres, 2008). In FR13A variety, Sub1A induces accumulation of DELLA proteins SLR1 and SLRL1 that inhibit GA responsiveness. Sub1 also regulates brassinosteroid (BR) synthesis genes DWF1/DWF4 that activates DELLA proteins to inhibit GA
responsiveness and shoot elongation which helps in prolonged submergence by conserving CHO content and ATP (Schmitz et al., 2011). Along with it, Sub1A acts as a negative feedback inhibitor of ethylene which in turn inhibits ethylene mediated GA responsiveness (Fukao & Bailey-Serres, 2008). In tobacco, ethylene-induced hyponastic petiole movement requires GA (Pierik et al., 2004). Also, ethylene-mediated enhancement of apical hook formation depends on GA in Arabidopsis seedlings (Vriezen et al., 2004). Leaf senescence is a major visible symptom in plants exposed to prolonged submergence. JA and SA are key phyto-regulators of molecular and biochemical processes of leaf senescence (Lim et al., 2007). Ethylene accelerates leaf senescence mediated by JA. Fukao et al. (2012) reported that SUB1A delays leaf senescence through inhibition of ethylene, JA and SA responsiveness in rice.

3. Indole-3-acetic acid (IAA) transport and perception are both affected by hypoxia and ethylene, leading to its accumulation in the stem base (Ecker, 1995; Vidoz et al., 2010). In flooded plants, the high level of ethylene stimulates the formation of adventitious roots either by increasing plant sensitivity to IAA or by stimulating the formation of root primordial (Visser et al., 1996). Both hormones act together in enlargement of the cortical cell layer in flooded tomatoes that stimulate stem hypertrophy. Auxin regulates multiple cellular processes like the differential expression of an auxin-induced K⁺ channel involved in osmotic regulation of growth (Fuchs et al., 2003), and auxin-induced activation of plasma membrane H1-ATPases leading to apoplastic acidification (Becker & Hedrich 2002) and expansin activation (Cosgrove, 2000). Emergence of adventitious roots is favored by cell-wall loosening through regulation of apoplastic pH or up-regulation of expansin genes, such as LeEXP1 in tomato (Zhao et al., 2009), which promotes cell-wall disassembly and cell enlargement.

Concluding remarks and future outlook

This review concludes that waterlogging influences a large number of traits in plants which regulates morphological, physiological and transcriptional changes during stress. There is now the utmost need to understand the diversity in gene behavior, architectural remodeling and biochemical alterations that can provide a wider space for improving growth and development of plants under these adverse stress conditions. The most potent aspect is the development of a mechanism that can counteract O₂ deficiency and depletion. Factors regulating ROS signaling and scavenging, as well as redox homeostasis, play an important role during hypoxia developed due to waterlogging or submergence. These factors can be identified and targeted for crop improvement. Targeting plasma membrane and organelle transporters could restore the ionic balance, O₂ permeability and metabolite level in the cellular level developed due to excess water. We can also target the modification at the genetic level using a conventional breeding approach to select waterlogging and submergence resistant morphological traits expressing constitutively in the propagated lines which can generate varieties that can tolerate or sustain waterlogging and submergence stress. Characterization of Sub1a, an ERF in rice, provides an insight into the survival mechanism under submergence. However, most of the Sub1a deficient varieties are still susceptible to excess water conditions unless they develop other mechanisms through other ERFs like SK1 and SK2. Large sets of transcriptome and microarray analysis needs to be conducted using contrasting varieties to identify certain conserved proteins across species, may be TFs that could assist the plant during waterlogging or submergence stress. In future, identification and characterization of waterlogging and submergence responsive genes and their upstream as well as downstream signaling cascade could help us to achieve the aim of generating stress-tolerant species under these adverse environmental conditions.

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