






Review Article

Multi-stress resilience in plants recovering from submergence

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Summary

Submergence limits plants' access to oxygen and light, causing massive changes in metabolism; after submergence, plants experience additional stresses, including reoxygenation, dehydration, photoinhibition and accelerated senescence. Plant responses to waterlogging and partial or complete submergence have been well studied, but our understanding of plant responses during post-submergence recovery remains limited. During post-submergence recovery, whether a plant can repair the damage caused by submergence and reoxygenation and re-activate key processes to continue to grow, determines whether the plant survives. Here, we summarize the challenges plants face when recovering from submergence, primarily focusing on studies of *Arabidopsis thaliana* and rice (*Oryza sativa*). We also highlight recent progress in elucidating the interplay among various regulatory pathways, compare post-hypoxia reoxygenation between plants and animals and provide new perspectives for future studies.

Introduction

Partial to complete submergence is detrimental to most terrestrial plants, and over the past six decades, flooding events have occurred with increasing frequency throughout the world due to global climate change (Bailey-Serres *et al.*, 2012a). The primary effect of submergence is restricted oxygen (O₂) and carbon dioxide (CO₂) availability in plant tissues due to the slow diffusion of gases in water (Bailey-Serres *et al.*, 2012a; Voesenek *et al.*, 2006). Furthermore, the low CO₂ availability and extremely low light levels in turbid floodwaters hamper photosynthesis in submerged plants (Bailey-Serres and Voesenek, 2008; Colmer and Voesenek, 2009). Therefore, submerged plants suffer from an energy and carbohydrate crisis that can lead to cell, organ and whole-plant death (Bailey-Serres and Voesenek, 2008; Colmer and Voesenek, 2009).

Responses to submergence have been characterized in various crops, wetland plants and model species (Bailey-Serres *et al.*, 2012b; Toulotte *et al.*, 2022). At the cellular level, plants initiate adaptive metabolic adjustments, such as managing the energy crisis by mobilizing carbohydrates, catabolizing sucrose and selectively translating key mRNAs; these responses determine submergence tolerance in plants (Bailey-Serres and Voesenek, 2008; Branco-Price *et al.*, 2008; Sorenson and Bailey-Serres, 2014; Voesenek and Bailey-Serres, 2015). In addition to cellular responses, plants have numerous morphological and anatomical adaptations that enhance survival of submergence. These include developing adventitious roots, producing

aerenchyma, forming gas films on leaf surfaces and enhancing shoot elongation (Bailey-Serres *et al.*, 2012b; Bailey-Serres and Voesenek, 2008; Colmer and Voesenek, 2009; Voesenek *et al.*, 2006; Voesenek and Bailey-Serres, 2015). These traits improve access to O₂, CO₂ and light, thus improving plant survival of submergence.

Hypoxia is a key part of submergence, and the discovery of the oxygen-sensing mechanism based on the oxygen-dependent N-end rule pathway-targeted turnover of ethylene response factor (ERF) VII group proteins in *Arabidopsis* (Gibbs *et al.*, 2011; Hartman *et al.*, 2019; Holdsworth *et al.*, 2020; Licausi *et al.*, 2011; Perata, 2020) improved our understanding of plant responses to hypoxia. Multiple signalling pathways related to plant survival under submergence, such as hypoxia signalling, energy signalling, ethylene signalling, nitric oxide signalling, reactive oxygen species (ROS) signalling and mitochondrial signalling, were recently discussed in some detail (Cho *et al.*, 2021; Hartman *et al.*, 2019; Hartman *et al.*, 2021; Meng *et al.*, 2020; Perata, 2020; Sasidharan *et al.*, 2018; Sasidharan and Voesenek, 2015; Shingaki-Wells *et al.*, 2014; Wagner *et al.*, 2018). Therefore, this review concentrates on post-submergence responses.

Due to natural drainage and effective agricultural management, flooding events are frequently transient. However, plants that survive submergence encounter multiple stresses after submergence, in the so-called post-submergence recovery phase (Shikov *et al.*, 2020; Tamang and Fukao, 2015; Yeung *et al.*, 2019). After the flood subsides, plants return to

atmospheric gas conditions and normal light conditions. This damages plant tissues that already suffered from submergence, causing reoxygenation stress, dehydration, photoinhibition and accelerated senescence (Shikov *et al.*, 2020; Tamang and Fukao, 2015; Yeung *et al.*, 2019). Moreover, the recovering plants must deal with the phytotoxins that accumulated during inundation or are newly produced upon de-submergence, as well as nutritional deficiency, both of which hamper the maintenance of cellular homeostasis (Shikov *et al.*, 2020; Tamang and Fukao, 2015; Yeung *et al.*, 2019). In addition, plants are particularly vulnerable to biotic stress during the recovery period (Yeung *et al.*, 2019).

Many recent studies have unravelled the molecular regulatory mechanisms associated with de-submergence. In this review, we discuss the possible causes of multiple stresses that plants suffer upon de-submergence. We also summarize recent major advances in our understanding of plant post-submergence recovery. Moreover, in view of the high conservation of oxygen-sensing systems in response to hypoxia (Doorly and Graciet, 2021; Gibbs and Holdsworth, 2020; Licausi *et al.*, 2020; Masson *et al.*, 2019), we discuss some similarities in reoxygenation stress responses between plants and animals. Finally, we highlight current knowledge about the complex trait of resilience to post-submergence stress and propose future research directions in this field.

Multiple challenges and coping mechanisms of plants in response to de-submergence

Reoxygenation stress

The sudden re-exposure to atmospheric oxygen following submergence can induce reoxygenation injury due to oxygen overload in cells that have acclimatized to prolonged oxygen deprivation. Post-submergence reoxygenation primarily triggers cellular oxidative damage due to the overproduction of ROS (Blokina *et al.*, 2003), including hydrogen peroxide (H_2O_2), singlet oxygen (1O_2), superoxide ($O_2^{\cdot-}$) and hydroxyl radical (OH^{\cdot}). ROS are by-products of aerobic metabolism that form via various metabolic pathways in different cellular compartments, such as chloroplasts, mitochondria and peroxisomes (Apel and Hirt, 2004; Mittler, 2017). When oxygen re-enters plant tissues, the rapidly restored respiratory capacity in mitochondria causes electron leakage in the mitochondrial electron transport chain (ETC) and proton leakage in the mitochondrial matrix, leading to a burst of ROS production (Chang *et al.*, 2012; Sasidharan *et al.*, 2018). The ROS burst is also associated with the activity of the plasma membrane-bound NADPH oxidase RBOHD, whose transcript abundance is strongly induced upon reoxygenation (Yeung *et al.*, 2018). Upon reillumination, photosynthetic metabolism can also trigger ROS formation in chloroplasts (Pospíšil, 2009).

The generation of environmental stress-induced ROS perturbs cellular redox homeostasis if the cell's antioxidant capacity is not sufficient to balance ROS production and scavenging, leading to oxidative stress (Mittler, 2002; Van Breusegem and Dat, 2006). The level of the membrane lipid peroxidation product malondialdehyde (MDA) is often used as an indirect measure of cellular oxidative damage. Increased MDA contents due to reoxygenation have been detected in *Arabidopsis* (Yeung *et al.*, 2018; Yuan *et al.*, 2017), rice (Fukao *et al.*, 2011) and soybean (*Glycine max*) seedlings (Tamang *et al.*, 2014), and in two wetland plants, *Alternanthera philoxeroides* and *Hemarthria altissima* (Luo *et al.*, 2012). Following de-submergence, ROS can also lead to

a transient burst of harmful acetaldehyde, as demonstrated in *A. philoxeroides* (Luo *et al.*, 2012).

Plants employ nonenzymatic and enzymatic ROS-scavenging mechanisms to cope with oxidative damage (Apel and Hirt, 2004; Blokhina *et al.*, 2003). Reoxygenation triggers the accumulation of nonenzymatic antioxidants including the major cellular redox buffers ascorbate and glutathione, which maintain cellular redox balance via the ascorbate–glutathione cycle following reoxygenation (Blokina *et al.*, 2000; Blokhina *et al.*, 2003; Yeung *et al.*, 2018; Yuan *et al.*, 2017). The enhanced activity of ROS-scavenging enzymes such as superoxide dismutase (SOD) upon reoxygenation plays important roles in oxidative stress resilience in many submergence-tolerant species (Blokina *et al.*, 2003; Borella *et al.*, 2019; Garnczarska *et al.*, 2004; Manjri *et al.*, 2017). For example, the submergence tolerance gene *SUB1A* in rice is important for recovery from submergence (Alpuerto *et al.*, 2016; Fukao *et al.*, 2011; Locke *et al.*, 2018) and a rice variety with the polygenic *SUB1* locus maintains higher ROS-scavenging activities and has lower lipid peroxidation following de-submergence, thereby limiting the cellular oxidative damage caused by excessive ROS production (Ella *et al.*, 2003a; Fukao *et al.*, 2011; Panda and Sarkar, 2012). In submergence-intolerant plant species, the activities of ROS-scavenging enzymes and antioxidant levels are minimal, often showing no changes during the post-submergence period (Blokina *et al.*, 2003).

Understanding the oxidative stress damage caused by reoxygenation would shed light on the balance between cellular ROS production and the scavenging capacity of sophisticated antioxidant systems. Accordingly, further studies on this topic will help us better understand the stress conditions encountered during reoxygenation and how different plants tolerate these conditions.

Tissue dehydration

During a flooding event, root function is severely damaged (Yamauchi *et al.*, 2018). Upon waterlogging, plant roots in water-saturated soils first experience oxygen deficiency, which leads to inhibited water transport through roots and a significant decrease in root hydraulic conductivity (*Lpr*) (Bramley and Tyerman, 2010; Colmer and Greenway, 2011). *Lpr* reflects the root's ability to take up water from the soil into the root stele for subsequent transport to the shoot (Vadez, 2014). In addition, soon after the flooding recedes, the root system continues to be surrounded by excess water, causing an imbalance between the potential for transpiration and water uptake (Striker, 2012).

Roots with significantly reduced *Lpr* usually have negative effects on water relations in shoots. For example, leaf water potential, an important indicator of plant water status, decreases in response to low *Lpr* under submergence (Else *et al.*, 1995; Else *et al.*, 2001). Therefore, as floodwaters subside, plants can experience an inherent water deficit, even though the soil contains sufficient water (Fukao *et al.*, 2011; Setter *et al.*, 2010; Yeung *et al.*, 2018). Plants exhibit rapid leaf rolling, wilting and decreased relative water content following de-submergence (Fukao *et al.*, 2011; Setter *et al.*, 2010; Yeung *et al.*, 2018; Yuan *et al.*, 2017).

Plants have some strategies to reduce transpirational water loss and maintain leaf water potential after floodwaters recede. For example, plants restrict stomatal conductance in leaves to prevent transpirational water loss and maintain leaf water content during post-submergence (Alpuerto *et al.*, 2016; Setter *et al.*, 2010; Yeung *et al.*, 2018). Abscisic acid (ABA) signalling modulates

multiple responses associated with dehydration stress (Fukao *et al.*, 2011). In the rice cultivar M202(*Sub1*), ABA responsiveness is promoted by the increased expression levels of ABA-regulated genes involved in acclimation to dehydration (Fukao *et al.*, 2011). Plants also limit water loss in leaves during post-submergence recovery via enhanced ROS-scavenging activity, which mitigates lipid peroxidation and membrane leakage (Yuan *et al.*, 2017).

Therefore, although it may seem paradoxical, plants must manage a potential water deficit through various mechanisms during post-submergence recovery.

Photoinhibition

Upon submergence in deep or turbid floodwaters, the limited light availability inhibits photosynthesis and plants acclimate to low light by altering the composition of the photosynthetic apparatus and chloroplast morphology. Upon de-submergence, photosynthetic acclimation to low light levels underwater rapidly changes in response to re-exposure to high light. Excessive ROS accumulation occurs in chloroplasts within the ETCs of photosystem II (PSII) and PSI during the light reactions under high-light stress (Gururani *et al.*, 2015). ROS can damage the photosynthetic apparatus, particularly PSII, which is one of the most susceptible components (Gururani *et al.*, 2015; Murata *et al.*, 2007). This leads to an imbalance in the photosynthetic redox signalling pathways and the inhibition of PSII damage repair, resulting in post-submergence photoinhibition (Gururani *et al.*, 2015; Murata *et al.*, 2007; Yeung *et al.*, 2019). During PSII photoinhibition, ROS (such as superoxide radicals and singlet oxygen) inhibit *de novo* synthesis of the essential PSII repair protein D1/PsbA, thus inactivating the PSII repair cycle (Gururani *et al.*, 2015). The suppression of CO₂ fixation inhibits the repair of PSII via increased H₂O₂ contents (Murata *et al.*, 2007) and reduced CO₂ diffusion caused by stomatal closure upon de-submergence can accelerate photoinhibition. The decline in activity of the photosynthetic apparatus via photoinhibition also hinders photosynthetic recovery and the restoration of carbon reserves.

The ability to maintain the functionality of the photosynthetic apparatus through rapid acclimation to changing light conditions is essential for post-submergence recovery. Non-photochemical quenching (NPQ) of chlorophyll fluorescence is a major photoprotective process that dissipates excess excitation energy within chlorophyll-containing complexes in PSII as heat (Gururani *et al.*, 2015; Murchie and Lawson, 2013). The maximal quantum yield of PSII (variable fluorescence/maximal fluorescence, *Fv/Fm*) is commonly used as a robust indicator of PSII efficiency (Murchie and Lawson, 2013). The inhibited NPQ and *Fv/Fm* recover gradually in some plant species when flooding is relieved (Alpuerto *et al.*, 2016; Luo *et al.*, 2009; Luo *et al.*, 2011; Pompeiano *et al.*, 2019; Sone and Sakagami, 2017).

During the post-submergence period, the time required to recover photosynthetic performance varies depending on the species, genotype and duration of inundation. The relatively tolerant Arabidopsis accession Lp2-6 exhibits full recovery of *Fv/Fm* values within 3 days following de-submergence (Yeung *et al.*, 2018). By contrast, the more sensitive accession Bay-0 failed to recover its *Fv/Fm* to normal levels (Yeung *et al.*, 2018). Lower *Fv/Fm* values indicate more photosystem II damage, which impedes replenishment of starch reserves post-submergence (Yeung *et al.*, 2018). Upon reillumination, M202(*Sub1*) rice maintains a greater capability for NPQ-mediated photoprotection and faster *Fv/Fm* recovery than submergence-intolerant rice; this

facilitates the rapid recovery of photosynthetic performance and energy reserve (Alpuerto *et al.*, 2016). However, Locke *et al.* (2018) found that *SUB1A* has a limited influence on the direct transcriptional regulation of nucleus-encoded subunits of the photosynthetic apparatus. Higher activities of ROS-scavenging systems were detected in submergence-tolerant rice line FR13A compared with intolerant IR42 during the recovery of submerged seedlings under excessive illumination (Ella *et al.*, 2003a).

Several factors play roles in restricted photosynthetic recovery in rice, such as chlorophyll degradation, decreased hydraulic conductivity and decreased Rubisco activity (Panda *et al.*, 2008; Sarkar and Panda, 2009; Setter *et al.*, 2010). Understanding these factors may enable efforts to improve tolerance to submergence and other stresses, such as high-light stress.

Accelerated senescence

Oxidative stress, dehydration and photoinhibition actuated by post-submergence accelerate leaf senescence in plants (Yeung *et al.*, 2019), and leaf yellowing caused by chlorophyll degradation is one obvious symptom of senescent leaves during recovery (Alpuerto *et al.*, 2016; Yeung *et al.*, 2018). During senescence, remobilization of nutrients from dying parts of plants to growing tissues is important for plant productivity, but the decreased levels of chlorophyll associated with the destruction of chloroplast function reduce photosynthetic efficiency (Gregersen *et al.*, 2013). The recovery of PSII photodamage helps prevent chlorophyll degradation (Kato *et al.*, 2014), which is reflected by increased *Fv/Fm* values. A decrease in *Fv/Fm* values reflecting chlorophyll degradation occurs in many species post-submergence (Luo *et al.*, 2018; Panda and Sarkar, 2012; Sone and Sakagami, 2017; Yeung *et al.*, 2018), pointing to a close relationship between impaired photosynthesis and accelerated senescence post-submergence.

Senescence triggered by submergence is further exacerbated upon de-submergence (Sone and Sakagami, 2017). Chlorophyll retained during submergence helps prevent leaf senescence and accelerates post-submergence growth recovery (Sone and Sakagami, 2017; Striker *et al.*, 2019). Indeed, inhibited leaf senescence, that is the maintenance of higher chlorophyll content and greener leaves, is a crucial feature of plants that survive flooding and plants with vigorous vitality following de-submergence. For example, submergence-tolerant rice cultivars with *SUB1A* undergo less chlorophyll breakdown in leaves during submergence and prolonged darkness compared with intolerant cultivars (Ella *et al.*, 2003b; Fukao *et al.*, 2006; Fukao *et al.*, 2012; Sarkar and Ray, 2016; Sone and Sakagami, 2017). *SUB1A* also restricts senescence during post-submergence recovery (Fukao *et al.*, 2012; Singh *et al.*, 2014; Sone and Sakagami, 2017). By contrast, submergence-intolerant rice cultivars that lack *SUB1A*, such as M202, IR42 and IR72442 exhibit rapid chlorophyll degradation during submergence and recovery (Ella *et al.*, 2003b; Fukao *et al.*, 2006; Sone *et al.*, 2012; Sone and Sakagami, 2017). The submergence-tolerant Arabidopsis accession Lp2-6, with higher chlorophyll contents in leaves, delays senescence by maintaining ROS homeostasis, stomatal aperture and leaf water potential homeostasis and restricting ABA and ethylene accumulation during de-submergence (Yeung *et al.*, 2018).

Cytokinin delays leaf senescence (Zwack and Rashotte, 2013) and accumulates in response to de-submergence (Huynh *et al.*, 2005; Tamang *et al.*, 2021). Delayed post-submergence

senescence was observed in *SAG12:ipt* transgenic plants, which accumulated more cytokinin than the wild type (Huynh *et al.*, 2005). After de-submergence, creeping bentgrass (*Agrostis stolonifera*) maintained higher chlorophyll levels when its leaves were sprayed with cytokinin and urea (Liu and Jiang, 2016).

The effects of submergence and post-submergence stress on photosynthesis (as described in the previous section) and ROS go hand-in-hand with the effects on chlorophyll degradation. A plant's ability to avoid a carbon-fixation catastrophe is crucial for its ability to survive post-submergence stress. However, disentangling cause from effect and identifying targets for improving this ability remain challenging.

Damage from accumulated toxins

In addition to affecting plants, flooding affects the soil microbiome, with potentially toxic consequences for plants. Decreased soil redox potential due to microbial respiration under flooded conditions provides an indicator of the chemical changes that occur during soil waterlogging (Parent *et al.*, 2008; Singh and Setter, 2017). The redox potential not only reflects the oxygen level, but it also significantly affects the concentrations and availability of various nutrients in flooded soil (Parent *et al.*, 2008; Setter *et al.*, 2009; Shabala *et al.*, 2014). Along with the rapid consumption of oxygen and the decrease in soil redox potential, microbial respiration employs other inorganic electron acceptors, specifically NO_3^- , Mn^{4+} , Fe^{3+} and SO_4^{2-} (Kirk *et al.*, 2003). Consequently, the concentrations of potentially toxic compounds, such as reduced forms of manganese (Mn^{2+}), iron (Fe^{2+}), H_2S and S^{2-} , increase in the soil during long-term submergence or soil waterlogging (Kirk *et al.*, 2003). Elemental toxicity induced by the accumulation of these compounds in plants through various forms of absorption and transport limits crop yields in specific soils exposed to flooding (Setter *et al.*, 2009; Singh and Setter, 2017; Zhang *et al.*, 2015).

Plant performance in response to elemental toxicity under flooding conditions depends on the soil type, as well as the plant species (Khabaz-Saberi *et al.*, 2006; Khabaz-Saberi *et al.*, 2012; Khabaz-Saberi and Rengel, 2010; Setter *et al.*, 2009). Several detoxification mechanisms that protect plants from elemental toxicity during submergence have been identified in many plant species (Shabala *et al.*, 2014; Zhang *et al.*, 2015). However, whether these mechanisms also function in post-submergence environments remains to be further studied. When floodwaters recede, plants still struggle with elemental toxicity, as well as reduced soil redox potential, which cannot be recovered in the short term. An increase in soil redox potential and a decrease in soil element toxicity occur upon de-submergence, but these processes occur slowly (up to 15–25 days) and are closely related to soil properties (Setter *et al.*, 2009; Yaduvanshi *et al.*, 2012).

In addition to inorganic toxins, plants must cope with secondary metabolite toxicity. During prolonged waterlogging, numerous short-chain aliphatic acids (acetic, propionic and butyric) and aromatic acids including phenolics accumulate in the soil (Shabala, 2011; Zhang *et al.*, 2015). The excessive accumulation of these metabolites influences a broad range of physiological processes, such as root and shoot growth, stomatal conductance, water potential and nutrient uptake (Shabala, 2011). Notably, damage due to phytotoxins in plants largely depends on the pH of the waterlogged soil and the rhizosphere (Shabala, 2011; Zhang *et al.*, 2015). The physiological strategies of plants that are adapted to high levels of phytotoxins are complex. Roots develop barriers to restrict the entry of these

phytotoxins (Armstrong and Armstrong, 2005). Oxidation in the rhizosphere due to increased radial oxygen loss from root tips and lateral roots is an essential trait for detoxification (Armstrong and Armstrong, 2005). Plants also employ various mechanisms to reduce the injury caused by phytotoxins, include limiting shoot growth, accelerating the senescence and abscission of older leaves, redistributing nutrients to young leaves and rapid stomatal closure (Zhang *et al.*, 2015).

The accumulation of metabolic products during acclimation to submergence may result in toxicity upon de-submergence. Upon reoxygenation, ethanol (the end-product of ethanolic fermentation remaining in tissues) is rapidly metabolized to acetaldehyde by the reverse reaction of alcohol dehydrogenase (ADH) and/or the peroxidation of ethanol by catalase (CAT) during the conversion of H_2O_2 to H_2O (Boamfa *et al.*, 2005; Meguro *et al.*, 2006). Excessive accumulation of acetaldehyde is harmful to plants due to its tendency to form acetaldehyde–DNA and acetaldehyde–protein adducts (Boamfa *et al.*, 2005; Perata *et al.*, 1992; Zhang *et al.*, 1997). Reduced ethanolic fermentation and ADH activity during recovery would help limit acetaldehyde production. Upon de-submergence, mitochondrial acetaldehyde dehydrogenase (ALDH) catalyses the conversion of acetaldehyde to acetate, which is less toxic and subsequently enters the tricarboxylic acid (TCA) cycle (Bailey-Serres and Voesenek, 2008; Meguro *et al.*, 2006; Tsuji *et al.*, 2003). A recent study in *Arabidopsis* found that the anion channel SLAH3 senses hypoxia-induced cytosolic acidosis and triggers a root anion efflux, boosting plant flooding stress responses (Lehmann *et al.*, 2021). Proton pump H^+ -ATPases, which can be switched on quickly, play a key role in preventing acidification of the vacuole (Shabala *et al.*, 2014). Nitrite ameliorates cytoplasmic acidification in maize (*Zea mays*) root segments during short-term anoxia (Libourel *et al.*, 2006).

These regulatory effects may play the same roles in submergence and de-submergence. However, the precise metabolic pathways mitigating injury caused by the excessive accumulation of the end products of anaerobic respiration during submergence and recovery remain to be fully elucidated. Breeding for tolerance to phytotoxins under flooding conditions and soil improvement would likely enhance the resilience of plants to both submergence and post-submergence conditions.

Nutritional deficiency

As mentioned above, phytotoxins prevent the adequate uptake of inorganic nutrients due to changes in membrane transport activity, and therefore, most plants suffer from inadequate nutrient uptake during prolonged submergence, leading to nutrient deficits in roots and shoots (Tamang and Fukao, 2015). Furthermore, hypoxic conditions make it challenging for plants to obtain transformable nutrients. With the decrease in redox potential, soil microorganisms use nitrate (NO_3^-), the dominant form of inorganic nitrogen in drained and aerated soil, as a primary alternative electron acceptor for respiration (Kirk *et al.*, 2003). As a result, soil nitrate is reduced to nitrite, various nitrous oxides and molecular nitrogen during the process of denitrification, all of which are unstable in waterlogged soil and cannot be used as a nitrogen source by plants.

Flooding-tolerant plant species use various strategies to ameliorate the negative effects of flooding on nutrient uptake. These include promoting root elongation and lateral root formation, facilitating infection by mycorrhizal fungi and modifying uptake kinetics (Elzenga and van Veen, 2010). Only a few studies have

evaluated the recovery of nutrient uptake and transport to the xylem upon re-aeration. Net K^+ uptake was shown to occur 4 h after re-aeration in wheat (*Triticum aestivum*) roots (Kuiper et al., 1994), indicating that hypoxic/anaerobic conditions impair membrane transport in roots and transport processes must be repaired after re-aeration (Colmer and Greenway, 2011). Plants reprogram their physiology to minimize nutrient requirements upon de-submergence. Post-submergence senescence contributes to the redistribution of nitrogen and helps maintain the nitrogen pool in plants. However, chlorophyll degradation is not beneficial to plant photosynthetic recovery or carbohydrate replenishment (Colmer and Greenway, 2011).

In the field, fertilizing after a flooding event increases the available nutrition in the soil and can improve crop resilience. The exogenous application of nitrogen helps promote stress resistance and post-submergence growth recovery. Nitrogen application was shown to increase antioxidant metabolism post-submergence in rice (Gautam et al., 2014a; Lal et al., 2015), soybean (Borella et al., 2019) and creeping bentgrass (Liu and Jiang, 2016), and productivity in rice (Gautam et al., 2017) and mung bean (*Vigna radiata*; Islam et al., 2019). Nitrogen and phosphorus application also helped maintain higher leaf chlorophyll content in rice (Gautam et al., 2014b; Gautam et al., 2016; Lal et al., 2015). Importantly, the responses of *SUB1* and non-*SUB1* rice cultivars to post-submergence nitrogen and phosphorus application are very different. Compared with non-*SUB1* cultivars, the *SUB1* cultivars showed higher nutrient uptake ability, biomass, grain yield and productivity after nitrogen and phosphorus application during the post-submergence phase (Gautam et al., 2017; Lal et al., 2015), indicating that *SUB1A* can improve the absorption and utilization of nutrients and rice resilience after the flood recedes. Consequently, growing crops with the submergence tolerance gene *SUB1A* (or perhaps other genes) managed with a reasonable fertilization regimen and timely drainage upon de-submergence can enhance crop survival and productivity.

Pathogen infection and insect attack

When a flood recedes, excessive water in the soil increases the relative humidity surrounding the plants; this high-humidity environment favours the growth of pathogens, making plants susceptible to diseases. Due to the high humidity, decreased plant biomass, and the escape of pathogens and pests from soaked and flushed soil, plants recovering from submergence injury are more vulnerable to pathogen infection and insect attack than they were before submergence (Brasier et al., 2003; Huber and Gillespie, 1992; Lytle and White, 2007; Rosenzweig et al., 2001).

Arabidopsis ERF-VII transcription factors play a variety of roles in disease resistance (Li et al., 2021; Tang and Liu, 2021; Zhao et al., 2012). Seedlings of the *SUB1A*-containing rice varieties show increased resistance to leaf blast caused by *Magnaporthe oryzae* and bacterial blight caused by *Xanthomonas oryzae* pv. *oryzae* during post-submergence recovery (Chaudhary et al., 2015a; Chaudhary et al., 2015b). In Arabidopsis, the ERF-VII transcription factors RAP2.2 and RAP2.3 positively regulate resistance to the necrotrophic fungal pathogen *Botrytis cinerea* (Li et al., 2021; Zhao et al., 2012). Interestingly, microarray analysis revealed that the constitutive expression of a stabilized form of *AtRAP2.12* could be used as an activator to regulate defence marker gene expression in plants under non-hypoxic conditions (Giuntoli et al., 2017). Accordingly, group VII ERFs are thought to integrate signals related to submergence and

disease resistance (Giuntoli and Perata, 2018). However, the exact mechanisms involved in this crosstalk need to be further investigated.

Submergence strongly activates many innate immunity marker genes and confers enhanced resistance to the virulent bacterial pathogen *Pseudomonas syringae* pv. *tomato* DC3000 (Pst DC3000; Hsu et al., 2013). The WRKY transcription factor WRKY22, which is strongly induced during the early stages of submergence, targets pattern recognition receptor (PRR)-related and microbial-associated molecular pattern (MAMP)-induced genes to form a transcriptional regulatory network associated with pathogen resistance to protect plants from pathogens during or after flooding (Hsu et al., 2013). In fact, many disease-resistance genes can be activated by hypoxia and submergence (Hsu et al., 2013; Huh, 2021; Lee et al., 2011; Tang and Liu, 2021; Wang et al., 2018; Yang et al., 2011). The involvement of the transcription factor WRKY33 in regulating plant resistance to necrotrophic pathogens has been well characterized in many previous studies. Recently, WRKY33 has been revealed to positively modulate hypoxia responses during submergence in Arabidopsis (Liu et al., 2021; Tang et al., 2021). The expression of *WRKY22*, as a pathogen-associated molecular pattern (PAMP)-triggered immunity (PTI)-responsive gene, is regulated by the L-type lectin receptor kinase LecRK-IX.2 during flg22-induced PTI responses (Luo et al., 2017). Hence, we believe that plant innate immune signalling likely contributes to immune responses and disease resistance during submergence and post-submergence.

The activation of innate immunity might have coevolved to allow plants to respond to submergence and to anticipate a higher risk of pathogen attack upon de-submergence (Hsu et al., 2013; Hsu and Shih, 2013). The concept of 'anticipating infection' was proposed to explain how plant innate immunity triggered by submergence protects plants against a higher probability of pathogen infection post-submergence (Hsu and Shih, 2013). The production of the plant hormones jasmonate (JA), salicylic acid (SA), ABA and ethylene, which are involved in plant defence responses, is rapidly induced following de-submergence (Chen et al., 2015; Tsai et al., 2014; Voesenek et al., 2003; Yeung et al., 2018; Yuan et al., 2017). These findings prompted us to propose that the accumulation of defence phytohormones may help plants cope with possible pathogen infection and insect attack post-submergence. In summary, we propose that plants employ two strategies to protect themselves against the higher risk of pathogen infection and insect attack after flooding: (1) submergence-triggered innate immunity, which protects plants against a higher probability of pathogen infection during subsequent de-submergence in order to 'anticipate infection'; and (2) the accumulation of defence phytohormones during post-submergence recovery, which regulates plant responses to post-submergence biotic stress via systemic signalling pathways.

In the field, many insects (including adults and larvae) exhibit a remarkable array of adaptations to hypoxia and thus can survive flooding (Hoback and Stanley, 2001). Submergence attenuates plant resistance to insect herbivores (Erb and Lu, 2013; Li et al., 2006). Therefore, submerged plants must rise to the challenge of limiting insect damage following de-submergence. However, the underlying regulatory and molecular details remain unclear. Interestingly, Arabidopsis WRKY22 promotes susceptibility to aphid (*Myzus persicae*) attack (Kloth et al., 2016). It would be interesting to investigate whether WRKY22, which is rapidly induced upon submergence, also regulates plant responses to insect feeding post-submergence.

Submergence and subsequent de-submergence make plants extremely vulnerable to pathogen and insect attack; bolstering disease and pest resistance is therefore an essential part of improving plant tolerance to flooding.

Recovery of metabolic homeostasis upon de-submergence

As floodwaters subside, the plant metabolic acclimation to submergence rapidly re-orientates to improve survival. Many metabolic processes re-adjust following reoxygenation, such as carbon and nitrogen metabolism, ion homeostasis and lipid metabolism (León *et al.*, 2021; Shikov *et al.*, 2020; Shingaki-Wells *et al.*, 2014; Tsai *et al.*, 2014). Plants also need to manage energy during recovery; avoiding cell death caused by a severe energy crisis requires optimized ATP production and reduced ATP consumption (Bailey-Serres *et al.*, 2012a; Bailey-Serres and Voeselek, 2008).

Soluble sugars and starch, which function as the initial sources of pyruvate in plants, are important for sustaining glycolysis, allowing cells to survive as long as they have a carbohydrate substrate (Bailey-Serres *et al.*, 2012a; Bailey-Serres and Voeselek, 2008). Carbohydrate reserves are indispensable for plant survival not only under oxygen deprivation but also during post-submergence recovery (Alpuerto *et al.*, 2016; Das *et al.*, 2005; Fukao *et al.*, 2006; Qin *et al.*, 2013). The higher levels of carbohydrate reserves in rice cultivars containing *SUB1A* contribute to redirecting metabolic flux and metabolic recovery from submergence injury upon de-submergence (Alpuerto *et al.*, 2016; Locke *et al.*, 2018). Greater starch reserves after submergence may provide more energy to meet the demands of reactivated metabolic processes in plant cells, especially in mitochondria and chloroplasts. During post-submergence recovery, submergence-intolerant plants with severely reduced photosynthetic capacity have a hard time replacing their starch reserves (Yeung *et al.*, 2018). Faster starch replacement and regrowth require rapid recovery of the photosynthetic apparatus and reactivation of photosynthesis (Liu *et al.*, 2015; Luo *et al.*, 2011; Yeung *et al.*, 2018).

Selective translation of a subset of mRNAs contributes to the reduced cellular protein synthesis and conservation of ATP during submergence (Branco-Price *et al.*, 2008; Sorenson and Bailey-Serres, 2014). Upon reoxygenation, the selective repression of translation is rapidly restored, resulting in a reconfiguration of central carbon and nitrogen metabolism (Branco-Price *et al.*, 2008; Sorenson and Bailey-Serres, 2014). The restraint of energy-consuming processes is rapidly reversed upon reoxygenation, indicating that the sensing of altered energy status and subsequent energy signalling modulate these processes (Branco-Price *et al.*, 2008).

Shingaki-Wells *et al.* (2014) stressed the importance of resetting mitochondrial metabolic processes during plant recovery from submergence. For example, upon de-submergence, mitochondrial ALDH converts acetaldehyde to the less toxic acetate, which enters the TCA cycle as a reaction substrate (Bailey-Serres and Voeselek, 2008; Meguro *et al.*, 2006; Tsuji *et al.*, 2003). In mitochondria, amino acid metabolism, respiratory chain function and alternative oxidase (AOX)-based alternative respiration facilitate the return to equilibrium during reoxygenation (Shingaki-Wells *et al.*, 2014).

To rapidly recover energy generation, TCA cycle intermediates must be replenished during reoxygenation (Tsai *et al.*, 2014; Tsai *et al.*, 2016). Ethylene signalling modulates induction of the

glutamate dehydrogenase (GDH) genes *GDH1* and *GDH2* upon reoxygenation. GDH is a key enzyme in the interconversion of glutamate and 2-oxoglutarate (Tsai *et al.*, 2016). Global metabolite analysis revealed that the deamination activity of GDH participates in TCA replenishment in *Medicago truncatula* seedlings and Arabidopsis during reoxygenation (Limami *et al.*, 2008; Tsai *et al.*, 2016). Disrupting GDH activity disturbs carbohydrate metabolism and delays energy regeneration during reoxygenation (Tsai *et al.*, 2016). Rice *SUB1A* might modulate the levels of metabolites and key enzymes to reorganize TCA cycle flux, thereby facilitating post-submergence recovery (Locke *et al.*, 2018). However, how ATP production recovers to normal upon de-submergence remains to be explored.

Membrane transport is impaired in oxygen-deficient roots, leading to insufficient ion flux for recovery (Colmer and Greenway, 2011; Greenway and Gibbs, 2003). The recovery of ion uptake and transport is necessary to balance ion homeostasis in plant cells. Reoxygenation triggers the up-regulation of many functional gene clusters associated with ion transport, which might influence ion homeostasis (Tsai *et al.*, 2014). Interestingly, plants reconfigure lipid metabolism during recovery from submergence (Wang *et al.*, 2016; Zhou *et al.*, 2020), suggesting that lipid composition helps fine-tune plant resilience during post-submergence recovery. The changes in lipid metabolism modulate ethylene signalling and ERF-VII-mediated hypoxia signalling (Savchenko *et al.*, 2019; Schmidt *et al.*, 2018; Wang *et al.*, 2016; Xie *et al.*, 2015a; Xie *et al.*, 2015b; Xie *et al.*, 2020; Xu *et al.*, 2020a; Xu *et al.*, 2020b; Zhou *et al.*, 2020), indicating that lipid remodelling plays essential roles in submergence tolerance.

The adjustment of the levels of several other compounds post-submergence, including arabinose, trehalose, alanine and phytohormones, to facilitate the recovery of plants from submergence was summarized in recent reviews (Bashar, 2018; León *et al.*, 2021; Shikov *et al.*, 2020; Yeung *et al.*, 2019). Although the current evidence provides novel insights into how plants achieve metabolic homeostasis, the complicated regulatory systems that mediate metabolic adjustments under post-submergence conditions remain to be further investigated.

Phytohormones in plant resilience to post-submergence stress

Several phytohormones increase upon de-submergence (Figure 1) and reoxygenation promotes the accumulation of transcripts encoding many phytohormone biosynthetic enzymes. For example, reoxygenation rapidly induces the expression of ethylene and JA biosynthetic genes in Arabidopsis (Tsai *et al.*, 2014; Yuan *et al.*, 2017). The regulatory mechanisms that underlie this process remain unclear, but the resulting rapid accumulation of ethylene and JA play essential roles in plants during recovery (Figure 1).

Ethylene signalling is involved in diverse cellular responses during reoxygenation, including maintaining antioxidant capacity and ROS homeostasis (Liu *et al.*, 2022), glutamate dehydrogenase-mediated metabolism (Tsai *et al.*, 2016) and plant responses to dehydration and senescence (Tsai *et al.*, 2014; Yeung *et al.*, 2018). The increased production of ethylene helps *Rumex palustris* maintain high rates of ethylene-dependent shoot elongation upon de-submergence (Voeselek *et al.*, 2003). During reoxygenation, ethylene enhances cell viability in root tips (Liu *et al.*, 2022). Although ethylene is considered to play an essential role in mediating recovery responses in plants, the higher production of ethylene is not beneficial for post-submergence

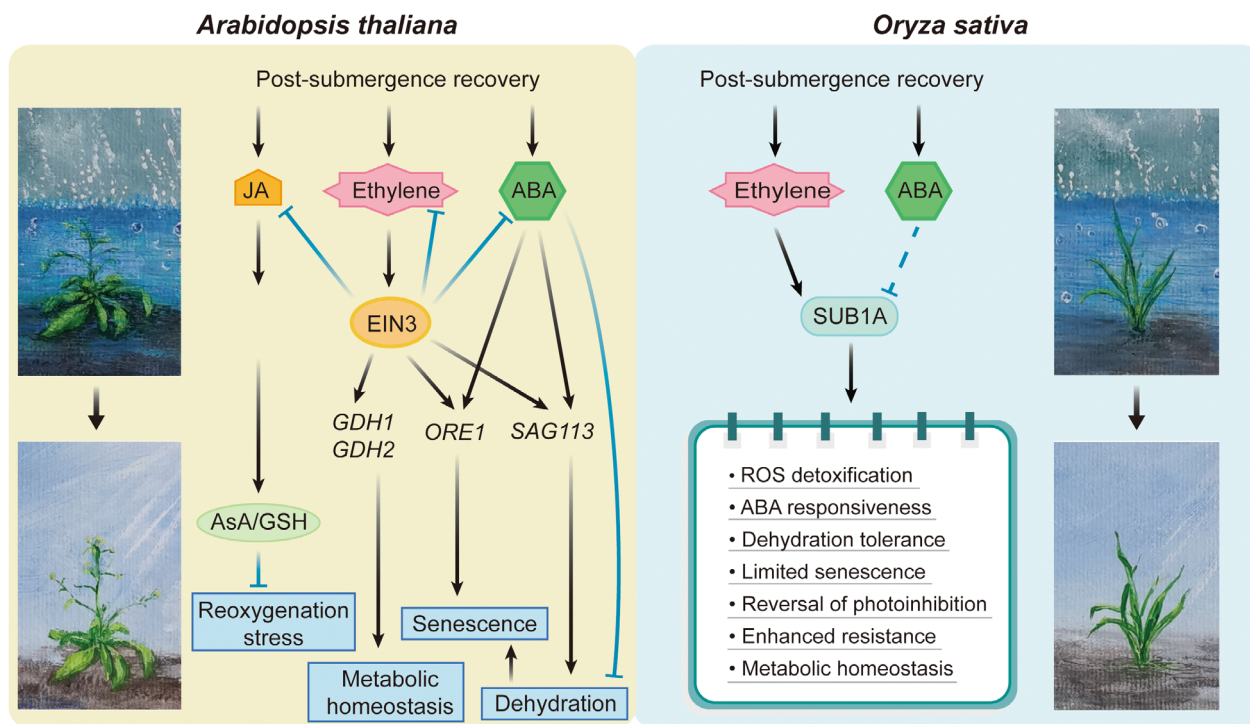


Figure 1 Hormones and transcription factors that regulate Arabidopsis and rice post-submergence stress responses. Black arrows indicate positive regulation and blue lines ending with perpendicular bars represent negative regulation. The blue dashed line ending with the vertical bar indicates a relationship that has not been fully elucidated.

recovery. The submergence-intolerant Arabidopsis accession Bay-0 produces significantly more ethylene than the tolerant accession Lp2-6 upon de-submergence, which is linked to visible shoot damage, leaf dehydration and accelerated senescence during recovery (Figure 1; Yeung *et al.*, 2018).

In addition to its roles in directly regulating recovery, ethylene signalling plays a major role in maintaining the balance of phytohormones during reoxygenation, including ethylene itself, as well as JA and ABA (Figure 1; Tsai *et al.*, 2014). The ethylene signalling-defective mutants *ein2-5* and *ein3 eil1* showed increased sensitivity to reoxygenation stress and enhanced expression of various ABA and JA biosynthesis and signalling genes (Tsai *et al.*, 2014). Based upon the multi-functionality of JA and the finding that ethylene inhibits the reoxygenation-triggered activation of JA biosynthetic and signalling pathways (Tsai *et al.*, 2014), JA responses may be fine-tuned by ethylene during reoxygenation. Ethylene is thought to restrict JA-regulated antioxidant biosynthesis when most cellular ROS have been eliminated post-submergence, allowing energy to be used on other biological processes (Yeung *et al.*, 2019). Exploring the underlying molecular mechanisms involving the synergistic and antagonistic interactions between ethylene and JA uncovered in these studies could provide a better understanding of the fine-tuning of ethylene and JA signalling post-submergence.

The rapid production of JA triggered by de-submergence prevents excessive ROS accumulation (Figure 1). This process is mediated by the core transcriptional regulator MYC2, which positively regulates antioxidant biosynthesis and accumulation (Yuan *et al.*, 2017). Nucleotidyl transferases, which function in nucleotide metabolism and amino acid activation, play vital roles in stress responses and recovery, possibly by altering nucleotide

metabolism and DNA damage repair (Khan and Komatsu, 2016). JA-induced changes in nucleotidyl transferase activity may facilitate the recovery of soybean roots from flooding stress (Khan and Komatsu, 2016).

ABA and SA signalling is also rapidly activated upon de-submergence (Yeung *et al.*, 2018; Yuan *et al.*, 2017). ABA regulates stomatal movement to limit water loss post-submergence (Yeung *et al.*, 2018). High ABA levels in the submergence-intolerant accession Bay-0 promote stomatal opening by up-regulating *SENESCENCE-ASSOCIATED GENE113* (*SAG113*), encoding a protein phosphatase 2C that inhibits stomatal closure to accelerate water loss and senescence, resulting in rapid water loss and leaf dehydration during recovery (Figure 1; Yeung *et al.*, 2018). This counterintuitive regulatory mechanism is likely mediated by the interplay between ABA and ethylene signalling post-submergence.

In Arabidopsis, ethylene suppresses ABA signalling during post-submergence recovery, but ethylene triggers ABA-independent transcription factors to help the plant deal with the dehydration caused by reoxygenation (Tsai *et al.*, 2014). Post-submergence- and ethylene-induced *SUB1A* augments ABA responsiveness at the gene expression level and restrains rapid dehydration following de-submergence in rice (Figure 1; Fukao *et al.*, 2011). In addition, dehydration tolerance regulated by *SUB1A* is also mediated by ABA-independent pathways (Fukao *et al.*, 2011). Besides playing essential roles in immunity and systemic acquired resistance, SA is involved in plant responses to abiotic stress (Khan *et al.*, 2015). However, the roles of SA in plant recovery from submergence are still unclear.

Hormonal regulatory networks play multiple important roles in regulating plant stress responses, which may also occur in the

post-submergence period. ABA protects the photosynthetic apparatus from heat stress (Gururani *et al.*, 2015). The transcription factor MYC2, encoding by a drought-responsive gene, is a positive regulator of ABA signalling (Kazan and Manners, 2013). ABA-induced PTP-like nucleotidase (PTPN)-mediated crosstalk between ABA signalling and ascorbate biosynthesis pathways positively regulates plant drought tolerance (Zhang *et al.*, 2020). These studies suggest that JA- and MYC2-mediated ascorbate biosynthesis pathways positively regulate dehydration tolerance in plants post-submergence. Therefore, similar findings may provide a new perspective on the hormonal regulatory networks that function in post-submergence responses.

Transcriptional reprogramming and transcription factors involved in regulating post-submergence resilience

In response to submergence, transcriptomic adjustments in the core network of genes associated with transcription, signalling cascades, and efficient energy generation and utilization occur in a wide range of plants (Bailey-Serres *et al.*, 2012a; Bailey-Serres and Voeseenek, 2010). De-submergence and post-anaerobiosis reoxygenation of plants also cause dramatic changes in gene transcription (Tsai *et al.*, 2014; Yeung *et al.*, 2018; Yuan *et al.*, 2017). RNA-seq showed that a complex transcriptional regulatory network is triggered in Arabidopsis upon reoxygenation, which plays an important role in maintaining cellular homeostasis and recovery from damage (Tsai *et al.*, 2014). The expression of genes involved in metabolism is fine-tuned during post-anaerobiosis reoxygenation, including genes involved in glycolysis, fermentation, TCA cycle replenishment, ion homeostasis and cellular biogenesis (Tsai *et al.*, 2014). Genes involved in metabolic processes and signalling pathways of plant hormones are induced during reoxygenation (Table 1 and Figure 1; Tsai *et al.*, 2014; Yuan *et al.*, 2017).

ETHYLENE INSENSITIVE3 (EIN3), a key transcription factor in the ethylene signalling pathway, activates targets that trigger various responses. The ethylene-insensitive mutant *ein3 eil1* is susceptible to sudden oxygen re-exposure and shows extensive cell damage (Tsai *et al.*, 2014). The abundance of EIN3 protein increases under reoxygenation stress; EIN3 directly regulates target genes to mediate recovery (Table 1 and Figure 1; Tsai *et al.*, 2016). The target gene *GDH2* and its homologue *GDH1*, which play essential roles in maintaining the balance of carbon and nitrogen during reoxygenation, are positively regulated by EIN3 (Chang *et al.*, 2013; Tsai *et al.*, 2016). *SAG113*, a target of EIN3, is induced by the higher ethylene and ABA production in regulating the early opening of leaf stomata upon de-submergence (Yeung *et al.*, 2018). The NAC (NAM, ATAF and CUC) transcription factor gene *ORESARA1* (*ORE1*), which is also a direct target of EIN3, encodes a positive regulator of leaf senescence that directly promotes the expression of a series of senescence-associated genes (Chang *et al.*, 2013; Matallana-Ramirez *et al.*, 2013; Qiu *et al.*, 2015). Elevated ethylene production and de-submergence promote the accumulation of *ORE1* transcript, and *ORE1* is responsible for higher chlorophyll breakdown, leading to senescence (Yeung *et al.*, 2018). Therefore, the EIN3 target genes *SAG113* and *ORE1* are specifically regulated in certain Arabidopsis accessions, with higher transcript abundance induced by ethylene in Bay-0 during post-submergence recovery (Table 1 and Figure 1; Yeung *et al.*, 2018).

The ERF-VII transcription factor SUB1A confers multi-stress resilience in rice post-submergence via multiple regulatory mechanisms (Table 1). De-submergence-induced *SUB1A* leads

to the enhanced transcript abundance of genes related to ABA responses and ROS detoxification to diminish desiccation and cellular oxidative damage (Fukao *et al.*, 2011). SUB1A delays senescence by inducing the expression of *DELAY OF THE ONSET OF SENESCENCE* (*OsDOS*) and repressing *CHLOROPLAST VESICULATION* (*OsCV*; Fukao *et al.*, 2012; Locke *et al.*, 2018). Transcriptome analysis of de-submerged plants demonstrated that SUB1A remodels the transcriptome and has a continuous impact on metabolite content to promote the recovery of metabolic homeostasis (Locke *et al.*, 2018).

Genes involved in JA biosynthesis and signalling are rapidly induced in Arabidopsis post-submergence, including the basic helix-loop-helix (bHLH) transcription factor gene *MYC2* (Kazan and Manners, 2013; Yuan *et al.*, 2017). Moreover, *VTC1* and *GSH1*, which encode rate-limiting enzymes of the ascorbate and glutathione biosynthesis pathways, respectively, are positively regulated by MYC2 as direct targets, leading to higher antioxidant production and enhanced tolerance to reoxygenation (Table 1 and Figure 1; Yuan *et al.*, 2017). Antagonistic crosstalk between JA and SA signalling has been demonstrated in Arabidopsis (Kazan and Manners, 2013). MYC2 appears to act as a negative regulator of SA signalling by inhibiting the expression of SA-related genes involved in recovery (Yuan *et al.*, 2017).

Transgenic Arabidopsis plants overexpressing sunflower (*Helianthus annuus*) *WRKY76* exhibited reduced leaf water loss and ultimately higher seed yields than the wild-type control upon de-submergence due to the induction of stomatal closure and higher cell membrane stability (Table 1; Raineri *et al.*, 2015). The strong and rapid induction of *WRKY22* mediates submergence-triggered resistance via its own downstream regulatory network (Table 1; Hsu *et al.*, 2013). Furthermore, the existence of *WRKY22*-regulated networks associated with various abiotic stresses suggests that this transcription factor acts as a universal node in plant responses to a spectrum of abiotic stresses (Hsu *et al.*, 2013). Rapid transcriptional reprogramming contributes to plant adaptability to post-submergence conditions. The expression of several transcription factor genes, such as *MYB*, *ERF* and *WRKY* genes, is regulated during post-submergence recovery (Tamang *et al.*, 2014; Yuan *et al.*, 2017). *WRKY33*, a positive regulator of the submergence response, is induced by recovery processes (Tang *et al.*, 2021). The accumulation of phosphorylated *WRKY33* induced by submergence is degraded by the ubiquitin E3 ligase SUBMERGENCE RESISTANT1 (SR1) upon de-submergence, leading to turn off the submergence response (Liu *et al.*, 2021). Consequently, it will be interesting to explore the regulatory mechanisms mediated by transcription factors in more detail. A combination of chromatin immunoprecipitation-sequencing (ChIP-seq) and transcriptome sequencing would likely contribute to our understanding of post-submergence resilience regulatory networks in plants.

Whole-genome single-base resolution profiling of DNA methylation by MethylC-seq showed significant differential DNA methylation in rice coleoptiles grown under anaerobic conditions and subsequent reoxygenation (Narsai *et al.*, 2017). Narsai *et al.* (2017) showed that the reversal of DNA methylation during reoxygenation may be a way for plants to reset the transcriptional state and prepare for rapid molecular changes that occur during cell division after anaerobic stress. León *et al.* (2021) discussed regulatory RNA-mediated plant responses during hypoxia, such as post-transcriptional alternative splicing and long non-coding RNAs (lncRNAs). At the same time, they pointed out that we

Table 1 Genes involved in plant regulatory networks that mediate post-submergence recovery

Gene	Species	General description	Function in post-submergence recovery	References
<i>SUB1A</i>	Rice (<i>Oryza sativa</i> L.)	A ERF-VII group gene Regulates submergence tolerance	Promotes recovery of metabolic homeostasis Promotes oxidative stress tolerance Promotes dehydration tolerance Promotes non-photochemical quenching (NPQ)-mediated photoprotection Inhibits chlorophyll degradation and leaf senescence Promotes resistance to leaf blast and bacterial blight	Alpuerto <i>et al.</i> (2016), Locke <i>et al.</i> (2018) Fukao <i>et al.</i> (2011) Fukao <i>et al.</i> (2011) Alpuerto <i>et al.</i> (2016) Singh <i>et al.</i> (2014), Sone and Sakagami (2017) Chaudhary <i>et al.</i> (2015a), Chaudhary <i>et al.</i> (2015b)
<i>EIN3</i>	<i>Arabidopsis thaliana</i>	An ethylene-dependent EIL family transcription factor gene	Mediates various responses modulated by ethylene	Tsai <i>et al.</i> (2014), Tsai <i>et al.</i> (2016)
<i>MYC2</i>	<i>Arabidopsis thaliana</i>	A jasmonate-activated bHLH transcription factor gene	Promotes reoxygenation stress tolerance	Yuan <i>et al.</i> (2017)
<i>ORE1</i>	<i>Arabidopsis thaliana</i>	A NAC (NAM, ATAF and CUC) transcription factor gene A direct target of EIN3	Accelerates chlorophyll breakdown and leaf senescence	Yeung <i>et al.</i> (2018)
<i>HaWRKY76</i>	Sunflower (<i>Helianthus annuus</i> L.)	A WRKY transcription factor gene	Promotes dehydration tolerance in transgenic <i>Arabidopsis</i> plants	Raineri <i>et al.</i> (2015)
<i>WRKY22</i>	<i>Arabidopsis thaliana</i>	A WRKY transcription factor gene	Promotes pathogen resistance	Hsu <i>et al.</i> (2013)
<i>GDH1</i>	<i>Arabidopsis thaliana</i>	Regulated by EIN3	Promote metabolic adjustment	Tsai <i>et al.</i> (2016)
<i>GDH2</i>		Encode subunits of glutamate dehydrogenase		
<i>VTC1</i>	<i>Arabidopsis thaliana</i>	Encodes a GDP-mannose pyrophosphorylase/mannose-1-pyrophosphatase involved in ascorbate biosynthesis	Direct target of MYC2 that mediates JA signalling Promotes reoxygenation stress tolerance	Yuan <i>et al.</i> (2017)
<i>GSH1</i>	<i>Arabidopsis thaliana</i>	Encodes glutamate-cysteine ligase, which catalyses the first and rate-limiting step of glutathione biosynthesis	Direct target of MYC2 that mediates JA signalling Promotes reoxygenation stress tolerance	Yuan <i>et al.</i> (2017)
<i>SAG113</i>	<i>Arabidopsis thaliana</i>	Encodes a Golgi-localized protein phosphatase 2C family protein	Mediates ABA and ethylene signalling Contributes to premature stomatal opening and subsequent dehydration and senescence	Yeung <i>et al.</i> (2018)

lack data on the involvement of regulatory RNA or RNA-related processes in reoxygenation. The epigenetic regulation of gene regulatory response to hypoxia has been summarized in detail (Lee and Bailey-Serres, 2021). An integrated analysis of data from a multi-omics study shows that progressively up-regulated and growth-associated transcripts are rapidly mobilized to ribosomes upon re-aeration (Lee and Bailey-Serres, 2019). Our understanding of the role of epigenetic regulation during reoxygenation is still minimal. Much work is needed to understand chromatin modifications and remodelling as well as the role of DNA methylation in reoxygenation recovery.

Integrated view of rice and *Arabidopsis* resilience to post-submergence stress

Water depth, duration, temperature and other factors during flooding affect submergence tolerance, the initiation of plant recovery and the effectiveness of coping strategies. In the face of the multiple challenges discussed above, plants will make similar changes to protect themselves, leading to reduced damage and restored growth. For example, the antioxidant mechanism that

regulates the response to reoxygenation stress is conserved. Rice, *Arabidopsis* and other species rapidly initiate evolutionarily conserved nonenzymatic and enzymatic ROS-scavenging systems to reduce oxidative stress. ABA signalling mediates the regulation of dehydration stress responses following submergence in both rice and *Arabidopsis* (Figure 1).

Group VII ERF transcription factors form a phylogenetic cluster that is conserved in angiosperms, coordinating signature responses to oxygen deficiency (Giuntoli and Perata, 2018). Upon re-aeration, *Arabidopsis* ERF-VIIs are rapidly degraded by the N-end rule pathway to release the hypoxic response (Gibbs *et al.*, 2011; Licausi *et al.*, 2011). As a master regulator of submergence tolerance in rice, *SUB1A*, which is homologous to *Arabidopsis* ERF-VIIs, also plays important roles during recovery (Table 1 and Figure 1) and it evades the N-end rule pathway for protein degradation (Gibbs *et al.*, 2011; Lin *et al.*, 2019) and maintains a high expression level post-submergence (Fukao *et al.*, 2011). It is important to note that some of the excellent traits of rice varieties containing *SUB1A* during the recovery period may be partly contributed by their flooding tolerance.

Some previous findings have hinted at this speculation. Better starch and soluble carbohydrate reserves in tolerant M202(*Sub1*) during submergence can benefit the rapid recovery of photosynthetic performance and energy reserve metabolism (Alpuerto *et al.*, 2016; Fukao *et al.*, 2006).

Arabidopsis APETALA2/ETHYLENE RESPONSIVE FACTOR (AP2/ERF) family transcription factors are involved in tolerance to a wide range of stresses. We believe that there are other AP2/ERF family members involved in regulating multiple stress resilience in *Arabidopsis* upon de-submergence. Ethylene and JA are involved in regulating post-submergence resilience (Figure 1); their biosynthesis pathways are conserved but their signalling pathways are specific in rice and *Arabidopsis* (Wan and Xin, 2022; Zhao *et al.*, 2021). This means that, in the recovering rice and *Arabidopsis*, resilience mediated by ethylene or JA may differ greatly even in response to a single stress.

Lessons from comparing post-hypoxia responses in plants and mammals

Several recent reviews summarize the remarkable similarity between the oxygen-sensing systems of plants and animals in response to hypoxia (Doorly and Graciet, 2021; Gibbs and Holdsworth, 2020; Licausi *et al.*, 2020; Masson *et al.*, 2019). Here, we explore similarities and differences between plants and animals during post-hypoxic reoxygenation (Figure 2). Both hypoxia and subsequent reoxygenation play indispensable roles in human pathophysiological processes because they occur in a wide variety of important clinical conditions (Li and Jackson, 2002). During post-hypoxic recovery, animals show cellular reoxygenation injuries such as impaired mitochondrial function, altered epithelial ion transport and increased cellular permeability. These injuries resemble those of plants with post-hypoxia damage (Figure 2). The generation of excess ROS is a shared characteristic of reoxygenation in animals and plants (Blokhina *et al.*, 2003).

In animals, enzymes including xanthine oxidase, ferryl haemoglobin and NADPH oxidase have been associated with reoxygenation-induced ROS formation and oxidative injury (Figure 2; Li and Jackson, 2002). Mitochondria are the main sources of ROS in both plants and animals. During reoxygenation, mitochondria generate excess $O_2^{\cdot-}$ and its dismutation product, H_2O_2 (Li and Jackson, 2002). A high level of plant mitochondrial biogenesis takes place in response to reoxygenation (Shingaki-Wells *et al.*, 2014). Treating *Arabidopsis* seedlings with mitochondrial ETC inhibitors provided evidence that mitochondria are the primary source of ROS during reoxygenation (Chang *et al.*, 2012). The NADPH oxidase RBOHD is also responsible for ROS bursts during post-submergence reoxygenation in *Arabidopsis* (Yeung *et al.*, 2018).

Oxidative stress triggered by reoxygenation causes cellular damage in both plants and animals (Figure 2). The antioxidant system is considered to be conserved in plants and animals; the antioxidant mechanisms inhibiting cellular reoxygenation injury are also similar. The enhanced activity of various ROS-scavenging enzymes such as SOD offers protection from oxidative stress damage in many plant species and animal cells (Blokhina *et al.*, 2003; Borella *et al.*, 2019; Garnczarska *et al.*, 2004; Manjri *et al.*, 2017). In animal cells, nonenzymatic antioxidants including ascorbate and glutathione also help maintain cellular redox balance by the ascorbate–glutathione cycle following reoxygenation (Chen *et al.*, 2007; Li and Jackson, 2002). Treatment with various secondary plant metabolites has been reported to improve the tolerance of animal cells to oxidative stress triggered

by reoxygenation. Sasanquasaponin, a biologically active ingredient extracted from the Chinese medicinal plant *Camellia oleifera* Abel, helps prevent cardiomyopathy under reoxygenation-induced oxidative stress by attenuating ROS generation and increasing the activities of endogenous antioxidants (Chen *et al.*, 2007). Flavonoids, a large group of phenolic plant chemicals with significant antioxidant properties, protected a human first-trimester trophoblast cell line from reoxygenation-induced oxidative stress (Ebegboni *et al.*, 2019). These findings suggest that some specific plant metabolites improve tolerance to oxidative stress during reoxygenation.

Hypoxia-induced autophagy, a highly conserved recycling system with fundamental physiological functions in eukaryotic cells, plays an important role in modulating cellular homeostasis in both animal cells and plants (Chen *et al.*, 2015; Kroemer *et al.*, 2010; Mazure and Pouysségur, 2010; Qi *et al.*, 2021; Yuan *et al.*, 2020). Autophagy is further activated following subsequent reoxygenation, which leads to programmed cell death and has some protective effects on recovering animal cells (Dosenko *et al.*, 2006; Sagrillo-Fagundes *et al.*, 2018). However, to date, little research has focused on the physiological functions of autophagy in plant responses to reoxygenation (Figure 2). Notably, excessive autophagy stimulated by the energy crisis and oxidative stress can promote cell death during post-hypoxia reoxygenation (Mazure and Pouysségur, 2010; Xiao *et al.*, 2015). During reoxygenation following hypoxia, mitochondrial function recovery occurs in both plants and mammals (Liu and Hajnóczky, 2011; Shingaki-Wells *et al.*, 2014). In *Arabidopsis*, MPK6 signalling is activated by reoxygenation-triggered mitochondrial ROS production (Chang *et al.*, 2012). A recent study suggested that MPK3 and MPK6 form a regulatory feedback loop with the phosphatidic acid biosynthetic pathway during hypoxia (Zhou *et al.*, 2022). Mitogen-activated protein kinase (MAPK) cascades are regarded as universal signal transduction modules in eukaryotes (Rodriguez *et al.*, 2010). The MAPK signalling pathways in animal cells are required for tolerance to post-hypoxia injury (Li and Jackson, 2002). A growing number of protein kinase signalling pathways in animals have been shown to be involved in reoxygenation. Therefore, conserved signalling pathways, including MAPK cascade signalling networks in plants and animals, are worth considering in future studies of reoxygenation (Figure 2).

Many valuable insights on adaptation to hypoxia and reoxygenation have been gained from research in animal cells. Considering the similarities, this knowledge could further our understanding of the acclimatization mechanisms of post-hypoxia reoxygenation in plants.

Conclusions and perspectives

As the last phase of plant tolerance to flooding, post-submergence recovery has gradually gained considerable attention in recent years. There is a consensus about the importance of monitoring plant responses post-submergence when assessing the flooding tolerance of specific crops. Studies of the re-adjustment and adaptation of plants during recovery have revealed some significant regulatory signalling pathways, downstream responses and effective recovery survival strategies. After a deluge, plants face multiple challenges and rapidly initiate multifaceted responses. Remarkably, these complex stresses are not isolated but are instead interrelated and interacting. Excessive ROS production triggered by reoxygenation not only causes oxidative damage to cells, but also promotes further damage,

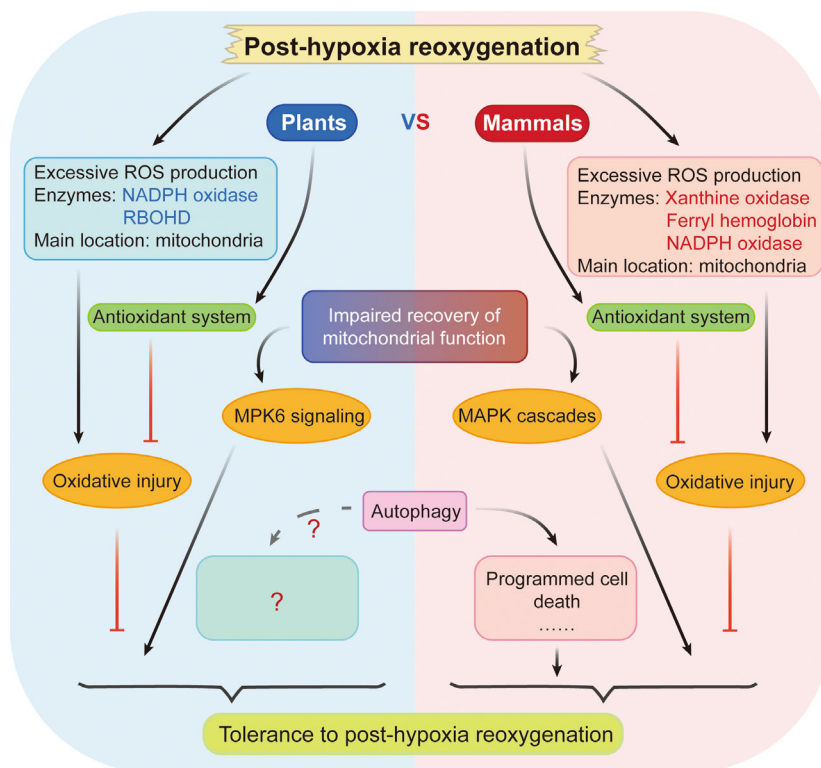


Figure 2 Comparison of post-hypoxic reoxygenation in plants and mammals. Excessive ROS production is a common feature of reoxygenation in plants and animals. The conserved antioxidant systems of animals and plants inhibit damage during cellular reoxygenation. Impaired recovery of mitochondrial function occurs in plants and mammals, activating downstream MAPK cascade signalling. Activation of autophagy protects recovering cells in mammals, but to date, little research has focused on autophagy in plant responses to reoxygenation. Positive and negative effects are illustrated by black arrows and red blunt-ended bars, respectively, and grey dashed arrows and red question marks indicate cases where the regulatory function is unknown at present.

including photoinhibition, dampened carbohydrate replenishment, dehydration stress and accelerated senescence (Yeung *et al.*, 2019). ROS accumulation can also be accelerated by reillumination stress and dehydration stress post-submergence (Fukao *et al.*, 2011; Yeung *et al.*, 2019). Oxidative stress is common in abiotic stress and recovery (Xu *et al.*, 2022). Hence, ROS might be the first molecules that hinder plant recovery. Fine-tuning of ROS metabolism by enhancing antioxidant activity and acquiring desiccation tolerance is an effective strategy to balance the redox status post-submergence.

Although the physiological traits associated with post-submergence have been extensively explored in many species, and some related molecular mechanisms have begun to be revealed, we are far from having a clear understanding of the molecular mechanisms controlling rapid, effective recovery from submergence. The hierarchical structure and interaction of diverse signals during recovery have not been established. Compared with the profound understanding of hypoxia sensing and acclimation responses to submergence, we still have a long way to go in exploring the mechanisms of post-submergence recovery.

Regrowth ability, which directly reflects the resilience of plants post-submergence, affects reproduction and yield after flooding events. After the floodwaters recede, the rapid development of new leaves and the maintenance of high production capacity have been observed in various recovering rice varieties and *Arabidopsis* accessions (Fukao *et al.*, 2006; Fukao *et al.*, 2011; Singh *et al.*, 2009; Singh *et al.*, 2014; Yeung *et al.*, 2018). These

findings suggest it may be fruitful to explore the natural genetic diversity of plants to further explore the relevant regulatory mechanisms. In addition, Toulotte *et al.* (2022) have presented the latest knowledge on flooding resilience mechanisms garnered from investigations of wild relatives of rice and maize, and suggested crop wild relatives as an invaluable reservoir of flooding stress tolerance traits. Therefore, we propose that improvements in crop resilience to post-submergence stress could be achieved by harnessing natural genetic diversity in breeding programmes.

Metabolites including plant hormones are important signalling molecules involved in regulating plant stress responses and development. Transcriptional regulatory networks mediated by transcription factors also play significant roles in transcriptional remodelling to improve plant resilience post-submergence. A greater focus on these two aspects of the post-submergence period could provide us with a better understanding of plant recovery regulatory networks. In recent years, several large-scale analyses of the dramatic cellular changes in plants in response to reoxygenation have been performed, including chromatin remodelling analysis, RNA assays and metabolomics assays (Lee and Bailey-Serres, 2019; Locke *et al.*, 2018; Tamang *et al.*, 2014; Tsai *et al.*, 2014). At present, innovations in genomics methods are producing many multi-scale high-resolution analyses of environmental responses (Akmakjian and Bailey-Serres, 2022). Integrative data from these and similar studies could provide us with new perspectives on post-submergence recovery. Therefore, taking full advantage of advanced multi-omics methods is key to solving

the mysteries of the post-submergence period and delivering a more comprehensive understanding of plant stress resilience during recovery.

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Conflicts of interest

No conflicts of interest are declared.

Author contributions

LB, LN and MX wrote the manuscript. RS, LAC and SX reviewed and edited the manuscript. All the authors read and approved the final manuscript.

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