



Tolerant mechanisms to O₂ deficiency under submergence conditions in plants

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Abstract

Wetland plants can tolerate long-term strict hypoxia and anoxic conditions and the subsequent re-oxidative stress compared to terrestrial plants. During O₂ deficiency, both wetland and terrestrial plants use NAD(P)⁺ and ATP that are produced during ethanol fermentation, sucrose degradation, and major amino acid metabolisms. The oxidation of NADH by non-phosphorylating pathways in the mitochondrial respiratory chain is common in both terrestrial and wetland plants. As the wetland plants enhance and combine these traits especially in their roots, they can survive under long-term hypoxic and anoxic stresses. Wetland plants show two contrasting strategies, low O₂ escape and low O₂ quiescence strategies (LOES and LOQS, respectively). Differences between two strategies are ascribed to the different signaling networks related to phytohormones. During O₂ deficiency, LOES-type plants show several unique traits such as shoot elongation, aerenchyma formation and leaf acclimation, whereas the LOQS-type plants cease their growth and save carbohydrate reserves. Many wetland plants utilize NH₄⁺ as the nitrogen (N) source without NH₄⁺-dependent respiratory increase, leading to efficient respiratory O₂ consumption in roots. In contrast, some wetland plants with high O₂ supply system efficiently use NO₃⁻ from the soil where nitrification occurs. The differences in the N utilization strategies relate to the different systems of anaerobic ATP production, the NO₂⁻-driven ATP production and fermentation. The different N utilization strategies are functionally related to the hypoxia or anoxia tolerance in the wetland plants.

Keywords Anoxia · Hypoxia · Low O₂ escape and low O₂ quiescence strategies (LOES and LOQS) · Nitrogen acquisition strategy · Re-oxidative stress · Respiration · Wetland plants

Introduction

O₂ deficiency in roots is often caused by frequent flooding during rains, submergence by excess rainfall, soil compaction, and increased microorganism activity caused by the rise in temperature. Prolonged submergence of the roots in

water can even lead to O₂ deficiency in shoots. These factors negatively affect the growth and survival of the whole plant, both in natural and agricultural ecosystems. The degree of O₂ deficiency in plant cells is classified as either hypoxia or anoxia. Hypoxia is characterized by restriction of aerobic metabolism, in which ATP production via the mitochondrial oxidative phosphorylation and NAD⁺ regeneration via the mitochondrial electron transport chain (mETC) are partially restricted. Anoxia is characterized by anaerobic metabolism, in which ATP is supplied solely via glycolysis, mitochondrial oxidative phosphorylation is completely inhibited, and the cellular ATP content is extremely low (Bailey-Serres and Voisenek 2008). Under these stress conditions, plants suffer from impairments that are caused by cell acidification and accumulation of reducing equivalents that lead to the production of reactive oxygen species (ROS) and reactive nitrogen species (RNS) (Hebelstrup and Møller 2015; Turkan 2018). Large amounts of ROS and RNS are produced under re-oxygenated conditions following the post-hypoxic

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and anoxic stresses, and they can further potentially damage the organelles. Thus, aerobic metabolism is suppressed during the recovery phase from O_2 deficiency owing to an inhibition of the metabolic functions (Bailey-Serres and Chang 2005; Fukao et al. 2011; Santosa et al. 2007).

Most terrestrial plants such as *Arabidopsis*, barley and maize, cannot survive long-term O_2 deficiency and severe anaerobic conditions even though they can survive under short-term stress with their hypoxia and anoxia tolerant responses. *Arabidopsis* under hypoxic conditions can regenerate NAD^+ via mETC and fermentation (Bucher et al. 1994; Dolferus et al. 2008; Ismond et al. 2003; Lasanthy-Kudahettige et al. 2007; Narsai and Whelan 2013), but glycolysis cannot continuously function under anoxic conditions (Lasanthy-Kudahettige et al. 2007; Loreti et al. 2005). The responses to O_2 deficiency in barley and maize have been examined to maintain their high yields at O_2 deficiency (Tollenaar and Lee 2002). They can oxidize $NAD(P)H$ to $NAD(P)^+$ via glycolysis and fermentation to avoid accumulation of reducing equivalents when they are exposed to hypoxia by flooding (Guglielminetti et al. 1995, 1999). They can metabolize RNS such as NO to maintain redox states and energy levels in the cytosol and mitochondria under hypoxia conditions (Igamberdiev and Hill 2004; Igamberdiev et al. 2006; Sowa et al. 1998). Maize can also form aerenchyma to aerate O_2 -deficient cells under hypoxic conditions similar to wetland plants (Armstrong and Armstrong 1994; Drew et al. 2000; Evans 2004; Hu et al. 2013). However, these plants cannot tolerate severe anoxia conditions that are caused by prolonged flooding and the following re-oxygenated condition after O_2 deficiency.

In contrast, wetland plants such as rice can tolerate severe anoxia and the following re-oxygenation conditions due to repeated flooding. This is because they possess high tolerant mechanisms such as advanced regulation of glycolysis in the cytosol, detoxification of ROS and RNS in the mitochondria, and maintenance of ATP production linked to NO detoxification in the mitochondria (Fukao et al. 2011; Huang et al. 2008; Voesenek and Bailey-Serres 2015). They can also acclimate to severely flooded soils through the O_2 supply from the aerial organ to O_2 -deficient organ. Their strategy is called low O_2 escape strategies (LOES). Plants with the LOES phenotypes can change their shoots and roots in response to O_2 deficiency such as shoot elongation, formation of aerenchyma, barriers to radial O_2 loss (ROL) from the roots, formation of adventitious roots (ARs), and maintenance of gas films on leaf surface (Colmer 2003; Eysholdt-Derzso and Sauter 2019; Sorrell and Hawes 2009; Winkel et al. 2013; Winkel et al. 2014). Some wetland plants show another strategy, low O_2 quiescence strategy (LOQS). Plants with the LOQS phenotypes can survive under severe O_2 -deficient conditions where their aerial parts are completely submerged by flooding. They can cease growth and

save their carbohydrate reserves until normal growth condition is recovered (Fukao and Bailey-Serres 2008; Fukao et al. 2006). These cellular and tissue level responses to O_2 deficiency in wetland plants permit their growth and survival under severe anoxic conditions.

Plant roots that are the sites of active nutrient absorption are often exposed to frequent and large fluctuations of O_2 concentration for short and long periods compared to the other organs. Wetland plants maintain their root activity by the aeration from the aerial organs to roots through the aerenchyma, and the available O_2 in their roots depends on their abilities of LOES which are enhanced under O_2 -deficient conditions. Many wetland species specialize in NH_4^+ utilization in habitats with a predominance of NH_4^+ . However, the wetland plants with the ability to supply O_2 from shoots to roots can utilize NO_3^- in addition to NH_4^+ , because of nitrification in their rhizosphere by active ROL from their root tips (Brix et al. 2002; Kirk and Kronzucker 2005). Moreover, it was recently reported that the root O_2 consumption strategies related to nitrogen (N) acquisition differ among species with differences in their ability to O_2 supply to the roots. The differences in strategies are associated with the differences in the O_2 demand by the aerobic respiration for root growth and N acquisition (Nakamura and Nakamura 2016; Nakamura et al. 2013). The N acquisition traits linked to the O_2 supply ability could relate to the hypoxia and anoxia tolerance in wild wetland species.

In this review, we summarize the previous findings on regulatory mechanisms of glycolysis, mitochondrial respiratory systems, primary metabolism in maintaining the energy production and homeostasis under O_2 -deficient and re-oxidative stress conditions, and developmental plasticity underlying acclimation to hypoxic and anoxic conditions in terrestrial, wild wetland, and cultivated species. Particularly, we aim to show different molecular level responses and different cellular and whole-plant level strategies between wetland species with long-term tolerance to O_2 -deficient conditions and terrestrial species with only short-term tolerance to the same conditions. Moreover, we summarize the effects of N sources (NH_4^+ and NO_3^-) on the root respiratory systems of wetland species, and thereafter, we discuss the characteristics of aerobic and anaerobic root respiration in wetland species associated with the utilization strategies of available inorganic N in their rhizosphere for maintaining energy production.

Regulatory mechanisms of fermentation and glycolysis under oxygen-deficient conditions

Under O_2 -deficient conditions, ATP production in most plants rapidly declines because the electron transfer in the mETC and flux in the tricarboxylic acid (TCA) cycle slow down and the transcripts encoding many of their enzymes

are down-regulated (Narsai et al. 2011). Even under low O₂ conditions, large amounts of energy are required for maintaining the various cellular components, including proteins, for survival (Mustroph and Albrecht 2003). Plants that are tolerant to O₂ deficiency have a high ATP production ability which is achieved by the enhancement of fermentation and glycolysis. They can regenerate NAD(P)⁺ from NAD(P)H accumulated by slow electron transport to maintain normal redox level under O₂-deficient conditions. In the first part of this section, we show mechanisms of ATP production and NAD(P)⁺ regeneration through the fermentation and glycolysis. In the latter part of this section, we show the regulations of glycolysis and cytosolic pH by the utilization of pyrophosphate (PP_i) which can act as a donor of phosphate for various metabolisms similarly to ATP (Shingaki-Wells et al. 2011).

Management of energy crisis through fermentation

Ethanol and lactate fermentation are two major metabolic pathways that produce energy under O₂-deficient conditions. Pyruvate derived from glycolysis is converted to ethanol through the coupled reactions catalyzed by pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH) in the ethanol fermentation pathway, and to lactate by lactate dehydrogenase (LDH) in the lactate fermentation pathway with the concomitant oxidation of NADH to NAD⁺ (Fig. 1). As the glycolytic flux to the ethanol fermentation pathway is higher than that to the lactate fermentation pathway in several plants, ethanol fermentation is considered to strongly contribute to low O₂ tolerance compared to lactate fermentation (Licausi and Perata 2009). A shift from pyruvate metabolism via the TCA cycle to the ethanol fermentation pathway is attributed to the K_m of PDC, which is similar to that of the accumulated pyruvate level under O₂-deficient conditions (Pronk et al. 1996). In rice plants, this shift is also associated with the inactivation of pyruvate dehydrogenase (PDH) by an up-regulation of PDH kinase (Marillia et al. 2003) and decreased translation of PDH mRNA (Branco-Price et al. 2008).

The ethanol fermentation pathway is controlled by the activity level and gene expression of PDC because the maximum catalytic activity of PDC is low (Drew 1997; Ismond et al. 2003; Mithran et al. 2014; Morrell et al. 1990). PDC-overexpressed terrestrial plants such as *Arabidopsis* and tobacco were reported to exhibit much higher ethanol concentration in their leaves compared with the wild types, and their survival rates under low O₂ conditions were enhanced (Bucher et al. 1994; Ismond et al. 2003).

In *Arabidopsis* plants, during O₂ deficiency, *PDC1* and *PDC2* are up-regulated in roots and leaves, respectively (Mithran et al. 2014). In rice plants, PDC is induced at both the transcript and protein levels during O₂ deficiency (Narsai

and Whelan 2013). Experiments examining the effects of PDC level on the submergence tolerance of rice had revealed that the correlation between PDC activity or expression and submergence tolerance was stronger in shoots that show high growth than those in roots and endosperms that show low growth at O₂ deficiency (Rahman et al. 2001). Moreover, rice varieties with high shoot elongation under anaerobic conditions showed active ethanol fermentation due to the high activity and gene expression of PDC in shoots, where the ethanol production was more active than that in roots under dark anaerobic conditions (Mustroph et al. 2006a, b). In contrast, there were no differences in root PDC activities between the varieties, and only a slight increase in activity was observed in submerged tolerant species under severe O₂ deficiency at night (Mohanty and Ong 2003; Rahman et al. 2001). These results suggest that the distribution range of wild wetland species is characterized by the fermentation abilities of the species due to the PDC activities in their shoots rather than those in their roots, and that the fermentation abilities in roots to survive in hypoxic soils are similar among species.

The activation of ADH does not lead to the acceleration of ethanol production in maize (Roberts et al. 1989). As with terrestrial species, in some rice cultivars, although the expressions of ADH genes (*ADH1* and *ADH2*) are not considered to be major determinants of the seedling vigor during hypoxic stress caused by submergence, these gene expressions respond to low O₂ stress (Vu et al. 2009). These reports suggest that ADH activity is not crucial in ethanol fermentation for energy compensation for anoxia tolerance. However, increased activity of ADH may be crucial in utilizing ethanol as a carbon (C) source under conditions where the plant experiences different stress at the same time or during re-oxygenation after flooding (Gibbs and Greenway 2003; Tsuji et al. 2003). Moreover, ADH has an essential role in germination and subsequent survival of the seedling at O₂ deficiency (Rahman et al. 2001).

Lactate fermentation also plays a crucial role in plant survival under anoxic conditions through the activity of LDH that reversibly catalyzes pyruvate and lactate (Fig. 1). Under O₂-deficient conditions, pyruvate is converted to lactate via LDH, and under re-oxygenated conditions after flooding, the accumulated lactate quickly disappears and the glycolytic flux is regulated by the regeneration of pyruvate from lactate (Germain et al. 1997a). Additionally, as lactate can induce cytosolic acidification and the cytosolic pH is adjusted to an optimal value for the PDC activity, lactate accumulation induces metabolic change from lactate fermentation to ethanol fermentation (Davies 1980). Dolferus et al. (2008) have also reported that increased LDH activity induces ethanol fermentation in *Arabidopsis*. Excessive accumulation of lactate causes cell death by a sharp decline of the cell pH. Thus, many plants possess lactate efflux

Fig. 1 Regulations of sugar catabolism, fermentation, glycolysis, and major amino acid metabolism associated with NAD(P)^+ regeneration and ATP production in terrestrial and wetland plants under O_2 -deficient conditions. Blue arrows and letters indicate the reactions and enzymes in the up-regulated pathways when the mitochondrial electron transport and the TCA-cycle flux decrease under O_2 -deficient conditions. Red letters indicate the regeneration of NAD(P)^+ from NAD(P)H . In rice plants, the blue pathways contribute to their tolerance to long-term O_2 deficiency compared with the terrestrial plants. Some wetland plants such as rice also have a high ability to optimally regulate the pyruvate level by activation of pyrophosphate (PP_i)-dependent phosphofructokinase (PFK- PP_i) and pyruvate phosphate dikinase (PPDK) that consume PP_i instead of ATP for energy conservation. Besides glycolysis, PP_i is consumed to regulate the cytosolic pH by the tonoplast H^+ -pumping pyrophosphatase (H^+ - PP_i ase) instead of H^+ -ATPase in wetland plants. Although two independent pathways for sucrose degradation contribute to the regulation of glycolytic flux in both terrestrial and wetland plants, the UDP-dependent sucrose synthase (SuSy) pathway is regarded as energetically more advantageous for survival under O_2 -deficient conditions than the invertase (INV) pathway because here, PP_i is utilized instead of ATP. Sugar supply to glycolysis through starch mobilization is observed in species with developed storage organs such as tuber, rhizome, and endosperm. In NAD(P)H regeneration during the metabolisms of 2-oxoglutarate and glutamate associated with γ -aminobutyric acid (GABA) production, the glutamate dehydrogenase (GDH) pathway without ATP consumption is more efficient in energy consumption than the NAD(P)H -dependent glutamine: 2-oxoglutarate aminotransferase (GOGAT) pathway with ATP consumption. The accumulation of some amino acids such as GABA, alanine, and glutamate play an important role in avoiding carbohydrate loss not only during O_2 -deficient conditions but also during the recovery phase of re-oxygenation after hypoxia/anoxia. Alanine accumulation by alanine aminotransferase (AlaAT) can operate non-circular TCA-cycle and gluconeogenesis under O_2 deficiency and re-oxygenation. Abbreviations are as follows: ADH, alcohol dehydrogenase; AlaAT, alanine aminotransferase; ALDH, acetaldehyde dehydrogenase; AspAT, aspartate aminotransferase; CoASH, coenzyme A; FK, fructokinase; GABA-T, GABA transaminase; GAD, glutamate decarboxylase; GHBDH, γ -aminobutyrate dehydrogenase; Glucose-1-P, glucose-1-phosphate; GS, glutamine synthetase; HKX, hexokinase; LDH, lactate dehydrogenase; MDH, malate dehydrogenase; PCK, phosphoenolpyruvate carboxykinase; PDC, pyruvate decarboxylase; PDH, pyruvate dehydrogenase; PEPC, phosphoenolpyruvate carboxylase; PFK, ATP-dependent phosphofructokinase; PFK- PP_i , PP_i -dependent phosphofructokinase; PGI, phosphoglucoisomerase; PGM, phosphoglucomutase; P_i , phosphate; PK, pyruvate kinase; PPDK, pyruvate P_i dikinase; SSADH, succinate semialdehyde dehydrogenase; Starch Pase, starch phosphorylase; TCA, tricarboxylic acid; UDP, uridine diphosphate; UGPPase, UDP-glucose pyrophosphorylase; UTP, uridine triphosphate

alanine and γ -aminobutyric acid (GABA) lead to the maintenance of glycolysis operation through the NAD(P)^+ regeneration and the stable preservation of carbohydrates under anaerobic conditions. Under post-anoxic conditions, metabolisms of GABA and alanine contribute to the avoidance from ROS accumulation and the recovery of aerobic metabolism during re-oxygenation, respectively. Terrestrial and wetland plants show different responses in starch mobilization, sucrose degradation and amino acid metabolisms to O_2 deficiency.

Starch mobilization in the maintenance of glycolysis A crucial point in the maintenance of glycolysis when plants are exposed to O_2 -deficient conditions is the efficient mobilization of the reserved carbohydrates (Dixon et al. 2006; Drew 1997; Gibbs and Greenway 2003; Licausi and Perata 2009; Sato et al. 2002; van Dongen et al. 2004) (Fig. 1). α -amylase and starch phosphorylase (Starch Pase) are induced by low O_2 and they convert starch to glucose and glucose-1 phosphate (P), respectively. These reactions are observed in storage organs of cereal grains, potato tubers and rhizomes for their germination and subsequent growth (Bucher and Kuhlemeier 1993; Das et al. 2000; Geigenberger 2003). Rice can germinate under low O_2 conditions due to the expression of α -amylase genes in its aleurone layer. Other terrestrial cereals such as wheat and barley cannot germinate under the same low O_2 conditions (Das et al. 2000; Guglielminetti et al. 1995, 1999; Narsai et al. 2009; Ricard et al. 1991). Among the three subfamilies of α -amylases genes (*AMY1A-C*, *AMY2A*, and *AMY3A-F*) in rice, *AMY3D* is anoxic-specific (Loreti et al. 2003; Park et al. 2010). Its induction under anoxia is repressed by high sugar levels, but is independent of gibberellin (GA) levels. This is because its promoter region lacks the distinctive cis-acting element that confers GA-responsiveness (Loreti et al. 2003; Park et al. 2010). In contrast, isoforms encoded by *AMY1A* are found in both aerobic and anaerobic seedlings, and *AMY1A* is induced by GA in seedlings under aerobic but not under anoxic conditions (Loreti et al. 2003; Morita et al. 1998). Thus, under aerobic conditions, GA-dependent activation of *AMY1A* maintains high sugar levels in the aleurone layer, and thereby *AMY3D* induction is prevented. The *AMY3D* expression depends on the cis-acting elements in its promoter region, named sugar repression core (*SRC*, Chen et al. 2006), and trans-acting transcription factor (TF), *MYBS1* (Lu et al. 2002). Moreover, *AMY3D* and *MYBS1* have been reported to be activated by the general regulator, sucrose non-fermenting receptor kinase 1A (*OsSnRK1*), which is promoted by calcineurin B-like interacting protein kinase 15 (*CIPK15*). They play a role in sugar and energy depletion signaling (Lee et al. 2014; Lu et al. 2002; Lu et al. 2007).

The mobilization of starch for constant carbohydrate supplementation under O_2 -deficient conditions is not common to all plants. Among terrestrial plants, this ability is limited to species with storage organs such as cereal grains and potato tubers (Arpagaus and Brändle 2000; Dixon et al. 2006; Guglielminetti et al. 1995). These plants can prevent starch depletion from their storage organs because they can sense the sugar level in their cells and subsequently down-regulate their metabolic rates (Arpagaus and Brändle 2000; Dixon et al. 2006). The mobilization of starch and regulation of sugar level at the germination and seedling growth stages have been poorly understood in wetland species other than rice plants. This metabolism may act as a crucial tolerance

mechanism in the germination and early development of wetland species because many wetland species with relatively large endosperms (members from the Gramineae and Cyperaceae families) (Kettenring and Galatowitsch 2007; Leck and Brock 2000; Wijte and Gallagher 1996) and developed rhizomes (members from the Nymphaeaceae and Menyanthaceae families) can grow in stagnant soil with low O₂ condition.

Two independent pathways for the sucrose degradation

The bidirectional UDP-dependent sucrose synthase (SuSy) and the unidirectional invertase (INV) are two distinct pathways for degradation of sucrose in plant cells (Fig. 1). SuSy consumes a net of one mol PP_i per one mol sucrose when UDP glucose and fructose are substrates for glycolysis. This is because the by-product of UDP glucose pyrophosphorylase, UTP, is used for the formation of phosphorylated fructose by fructokinase (FK), and simultaneously ATP is regenerated from ADP via NDP kinase (Bailey-Serres and Voeselek 2008; Guglielminetti et al. 1999). In contrast to the consumption of PP_i by SuSy, the INV reaction involves two mols ATP per mol sucrose (Mustrup et al. 2005). Therefore, SuSy is regarded as a more energetically advantageous pathway in various species for survival under O₂-deficient conditions than INV. Indeed, transgenic potato tubers with elevated INV activity were unable to maintain ATP levels under low O₂ conditions (8% O₂) (Bologa et al. 2003).

Responses of activities and transcriptions to low O₂ conditions differ between SuSy and INV. The activity and mRNA transcript level of SuSy are rapidly increased by sugar starvation, in contrast to the constitutive expression of INV in various terrestrial and wetland plants (Branco-Price et al. 2008; Koch 2004; Lasanthi-Kudahettige et al. 2007; Loreti et al. 2005). Comparative analysis of gene inductions and protein expressions with or without sucrose addition revealed that SuSy gene expression is up-regulated by sensing sugar starvation as signals (Contento et al. 2004; Liu et al. 2010; Loreti et al. 2005; Nicolai et al. 2006; Rolland et al. 2006). In rice, six SuSy isoforms localized in roots, mesophylls, and phloem are tissue-specifically expressed at different developmental stages (Hirose et al. 2008; Wang et al. 1999). Particularly, the expression of *SUS2* significantly increases in germinating seeds and growing seedlings under anoxic conditions (Hirose et al. 2008), indicating that *SUS2* can serve not only as a housekeeper but also as the initial reaction of sucrose degradation during stress. In addition to the single hypoxia-inducible SuSy isoform, multi-expressions of the SuSy isoforms with functional redundancy are required to ensure low O₂ tolerance in several species of both terrestrial and wetland plants (Bieniawska et al. 2007; Hirose et al. 2008; Wang et al. 1999).

INV catalyzes sucrose into fructose and glucose, which are then phosphorylated by hexokinase (HXK) or FK to be channeled into the glycolytic pathway (Licausi and Perata 2009) (Fig. 1). The glycolytic flux is also regulated by the activation of the INV pathway, but the main pathway of sucrose degradation under aerobic conditions may be the SuSy pathway (Fig. 1). This regulation of glycolysis is noted not only in the roots of terrestrial crops such as maize and tomato (Bouny and Saglio 1996; Germain et al. 1997b) but also in the seedlings of rice (Cho et al. 2006; Guglielminetti et al. 2006). In rice plants exposed to anoxia, *OsFK2* and *OsHXK7* are induced by sensing sucrose starvation as signals (Cho et al. 2006; Guglielminetti et al. 2006; Lasanthi-Kudahettige et al. 2007). Other isoforms, *OsHXK5* and *OsHXK6*, dual-targeted to the mitochondria and nucleus, also act as glucose sensors (Cho et al. 2009; Narsai and Whelan 2013). They directly regulate the downstream factors including CIPK15, which in turn regulate the representative α -AMY3 gene (*RAMY3D*) and *ADH2* expression in rice under low O₂ conditions (Yim et al. 2012).

Metabolism of typical amino acids linked to glycolysis regulation under O₂-deficient conditions

At low O₂, NAD(P)⁺ regeneration can be achieved by amino acid metabolisms such as the metabolism of 2-oxoglutarate and glutamate associated with the production of GABA (Fig. 1). The synthetic pathway of GABA through the glutamate decarboxylation by glutamate decarboxylase (GDC) with H⁺ consumption can contribute to the counteraction of cytosolic acidification caused by anoxic stress (Aurisano et al. 1995). The metabolism of 2-oxoglutarate and glutamate is promoted through the glutamine synthetase (GS)-glutamine oxoglutarate aminotransferase (GOGAT) pathway or the glutamate dehydrogenase (GDH) pathway. In the former, GS and GOGAT catalyze the conversion of glutamine to glutamate with 2-oxoglutarate incorporation, whereas in the latter GDH reversibly catalyzes the reaction between 2-oxoglutarate and glutamate (Narsai et al. 2009; Rocha et al. 2010; Shingaki-Wells et al. 2011) (Fig. 1). The GDH pathway does not consume ATP in the conversion of 2-oxoglutarate to glutamate, while the GS-GOGAT pathway consumes one ATP mol per glutamate mol for the conversion of glutamine to glutamate (Gibbs and Greenway 2003) (Fig. 1). Therefore, the GDH pathway is more efficient in energy consumption. Moreover, increased glutamate can act as an amino group donor in the aspartate transamination by aspartate aminotransferase (AspAT) for the production of oxaloacetate, an intermediate product in the TCA cycle during anoxia (Fig. 1). Oxaloacetate is then converted to malate by malate dehydrogenase with NAD(P)⁺ regeneration (Bailey-Serres and Voeselek 2008). Glutamate is simultaneously incorporated into the pathway by alanine aminotransferase (AlaAT) (Bailey-Serres and Voeselek 2008; Ricoult et al. 2006)

(Fig. 1). Under hypoxia, strong induction of mRNA levels and enzymatic activities of AspAT, AlaAT, and GDH in the cytosol and mitochondria have been reported in Arabidopsis and rice plants (Klok et al. 2002; Lasanthi-Kudahettige et al. 2007; Liu et al. 2005; Loreti et al. 2005; Mustroph et al. 2010; Narsai and Whelan 2013; Narsai et al. 2011). Thus, the synthesis of these amino acids may contribute to the regulation of glycolysis through NAD(P)⁺ regeneration in both terrestrial and wetland species.

Metabolisms of GABA and alanine seem to play important roles for plants in survival during low O₂ stress and re-oxygenation. Kreuzwieser and Rennenberg (2014) have reported that the supply of carbohydrates to amino acid metabolism in shoots and roots is a key process that helps plants survive hypoxia. The metabolism of these amino acids does not result in carbohydrate loss compared with fermentation. In Arabidopsis, the importance of organ-specific response in these advantageous amino acid metabolisms has been pointed out. High GABA accumulation in roots was observed under hypoxia compared with that in shoots, while alanine accumulation was observed in both organs (Mustroph et al. 2014). Transcriptome and metabolome analyses of flooding-intolerant Arabidopsis and flooding-tolerant rice and poplar exposed to anoxia indicated that the accumulation of alanine and succinate and the increased activities of fermentation enzymes were observed in all the species, but that the transcriptional regulations of amino acid metabolism and anaerobic fermentation were different among species (Narsai and Whelan 2013; Narsai et al. 2011). Plant species may have specific mechanisms for signal transduction and post-transcriptional regulation in the amino acid and carbohydrate metabolisms in roots and shoots.

The increased accumulation of GABA under anoxia is metabolized by GABA transaminase (GABA-T) to succinic semialdehyde coupling with consumption of 2-oxoglutarate and additional conversion of pyruvate to alanine (Fig. 1). In the subsequent reaction, succinic semialdehyde is converted either to γ -hydroxybutyrate by the NAD(P)H-consuming reaction catalyzed by GABA dehydrogenase (GHBDH) or to succinate that can be channeled to the TCA cycle by succinate semialdehyde dehydrogenase (SSADH) by the NAD⁺-consuming reaction (Fig. 1). Although the high activity of SSADH with NAD⁺ consumption is thought to be disadvantageous for glycolytic regulation under hypoxia, this enzyme can function as one component of the bypass of the TCA cycle (GABA-shunt) to decrease ROS accumulation under re-oxygenation conditions (Bouche et al. 2003) (Fig. 1). Indeed, higher accumulation of SSADH protein was observed under re-oxygenation conditions in Arabidopsis (Bouche et al. 2003).

Besides anoxic stress, post-anoxic stress can also severely damage plant growth owing to large amounts of ROS that are produced in the cells. Particularly, wetland plants such as

rice plants often suffer from post-anoxic stress after frequent floods; they have been reported to exhibit significant transcript reprogramming, which rapidly increased the expression of genes encoding TCA-cycle enzymes and levels of metabolites including citrate and 2-oxoglutarate to restore aerobic growth under post-anoxic conditions (Narsai et al. 2009). Moreover, large amounts of alanine generated by AlaAT under anaerobic conditions help plants to survive under subsequent re-oxygenation conditions because alanine can be transported through the xylem as a transportable energy source (De Sousa and Sodek 2003). AlaAT can convert the transported alanine into pyruvate, which can be used in gluconeogenesis or metabolized to acetyl-CoA (Fig. 1); both processes are important for aerobic metabolism during re-oxygenation (Rocha et al. 2010; Shingaki-Wells et al. 2014). In contrast, coleoptiles of anoxia-intolerant wheat seedlings cannot accumulate alanine when they are subjected to anoxia (Shingaki-Wells et al. 2011). These findings suggest that alanine accumulation by activated AlaAT in the flood-tolerant species plays an important role in their survival not only during hypoxia but also during the recovery phase of re-oxygenation after hypoxia.

Utilization of available PP_i as the phosphate donor instead of ATP It has been assumed that PP_i is particularly favored as a phosphoryl donor compared with ATP in anoxic tissues where the cytosol is acidic (Davies et al. 1993; Felle 2005). Thus, PP_i can serve an alternative energy source instead of ATP, and is utilized to maintain the glycolysis flux and regulation of cytosolic pH under low O₂ conditions where ATP levels are low.

In glycolysis, the enzymes with reversible reactions, PP_i-dependent phosphofructokinase (PFK-PP_i) and pyruvate phosphate dikinase (PPDK), can function instead of ATP-dependent phosphofructokinase (PFK-ATP) and pyruvate kinase (PK), respectively (Fig. 1). As PFK-PP_i can catalyze fructose 6-P without consumption of ATP, the PFK-PP_i function can increase the net ATP production in anoxia-tolerant plants (Huang et al. 2008; Plaxton and Podestá 2006) (Fig. 1). In rice seedlings, the enzymatic activity of PFK-PP_i is dramatically increased by 15-fold after 24 h in anoxia (Gibbs et al. 2000; Kato-Noguchi 2002; Mertens et al. 1990). The expression of annotated PFK-PP_i genes in anoxic rice coleoptiles is complex. Some are down-regulated and others are up-regulated (Lasanthi-Kudahettige et al. 2007). In contrast, gene expression and protein amounts of the cytosol-type and plastid-type PPDKs in rice are up-regulated under anoxia. Especially the expression of cytosolic-type PPDK is up-regulated by 365-fold when the plants are exposed to anoxia (Lasanthi-Kudahettige et al. 2007; Moons et al. 1998; Shingaki-Wells et al. 2011) and is higher in roots than that in shoots (Huang et al. 2008). This suggests that roots have a higher ability to enhance anoxia tolerance than shoots

because roots often experience more frequent fluctuations of O_2 concentration than shoots.

Induction of PFK- PP_i and PPDK is controlled by the cytosolic PP_i content under short- and long-term anoxia, but not by the exogenous substrates such as starch and sucrose (Huang et al. 2008). While the PFK-ATP activity is rate-limiting for glycolysis in short-term anoxia, PFK- PP_i can compensate for the ATP limitation by using PP_i . In such a situation, PP_i can be provided by a reaction cycle catalyzed by both PPDK and PK. This would accelerate the glycolytic flux and supply energy for survival at the early phase of anoxia. In contrast, if the plants are exposed to long-term anoxia, glycolysis may need to be down-regulated to conserve carbohydrates. Thus, PFK- PP_i and PPDK may regulate the PP_i level to slow down the net glycolytic flux for survival under long-term anoxia, and thereby the direction of glycolysis is changed to gluconeogenesis. Some reports indicate that this functional regulation of PP_i level may strongly contribute towards maintaining glycolysis under severe anoxic conditions where the ethanol fermentation is declined (Colmer et al. 2001; Huang et al. 2008; Kato-Noguchi 2002; Loreti et al. 2005). Therefore, enzyme-mediated reactions can contribute to low O_2 tolerance in either direction, towards glycolysis or gluconeogenesis, although it is difficult to experimentally show the reaction directions by PFK- PP_i and PPDK because of their small free energy values (ΔG) (Huang et al. 2008).

Gene expressions of PFK- PP_i and PPDK in anoxia-intolerant Arabidopsis did not show significant changes in anoxia (Lasanthi-Kudahettige et al. 2007; Loreti et al. 2005). Under these conditions, the gene encoding PFK- PP_i was up-regulated by 1.9-fold, and PPDK by only 1.1–1.7-fold. This change in PPDK in Arabidopsis was much less than that in the cytosolic-type PPDK in rice plants. In rice plants, PFK- PP_i and tonoplast H^+ - PP_i ase were induced during phosphate (P_i) deficiency, but the change in PPDK during P_i deficiency is unclear (Plaxton 2004). Interestingly, even under various stress environments where the levels of the nucleoside triphosphate (NTP) pools including P_i , ATP, and ADP were significantly decreased, the PP_i levels were relatively stable in rice plants (Plaxton 2004). Especially the PP_i concentrations in coleoptiles and cultured cells of rice plants were similar between anoxic and aerated conditions (Kato-Noguchi 2002; Mohanty et al. 1993). These results suggest that the stable level of PP_i in rice plants supports a stable response to the crisis in energy production by a sudden O_2 decrease via PP_i -dependent enzymes. Moreover, the gene expression of inorganic pyrophosphatase (PP_i ase) in rice coleoptile was significantly down-regulated by 35-fold when they were exposed to anoxic conditions, whereas the gene expression of inorganic PP_i ases in Arabidopsis was unchanged or slightly up-regulated under anoxic conditions (Lasanthi-Kudahettige et al. 2007). Consequently, in rice

plants under anoxic conditions, PP_i is not degraded by inorganic PP_i ase and large amounts of PP_i can be used for the other essential processes (Huang et al. 2008). In contrast, in Arabidopsis cells under anoxic conditions, the PP_i content decreases and the plants suffer severe energy deficiency because solute transport across the tonoplast decreases and the cytosol pH is acidic, resulting in ultimately cell death (Fukao and Bailey-Serres 2004). The roles of PP_i -dependent enzymes in wild wetland plants, other than rice plants, are restricted to a few studies in which the gene expression of cytosolic PPDK in *Eleocharis vivipara* and the activity and induction of PFK- PP_i and PPDK in *Potamogeton pectinatus* were examined (Dixon et al. 2006; Summers et al. 2000). As these amphibious plants grow under various O_2 conditions from land to deep-water wetland, it is assumed that many wild wetland plants may commonly utilize PP_i -dependent enzymes in response to changes in the O_2 availability.

Besides glycolysis, many plants consume PP_i to regulate the cytosolic pH under O_2 -deficient conditions by the tonoplast H^+ -pumping pyrophosphatase (H^+ - PP_i ase) instead of H^+ -ATPase (Fig. 1). This can support the essential process of pH regulation even under ATP-deficient conditions. Anoxia-tolerant rice can suppress the pH decline in anoxia to half of that in the normal conditions, while anoxia-intolerant wheat and Arabidopsis suffer severe pH decline during anoxia (Lasanthi-Kudahettige et al. 2007; Loreti et al. 2005; Menegus et al. 1991). In rice plants, the activity of the tonoplast H^+ - PP_i ase was increased by 75-fold after 6 days in anoxia (Carystinos et al. 1995), and the gene (*Os02g55890*) encoding H^+ - PP_i ase was up-regulated by 35-fold in anoxia (Lasanthi-Kudahettige et al. 2007).

Mitochondrial metabolic adaptation to O_2 deficiency

ROS (e.g., H_2O_2 and O_2^-) and RNS (e.g., NO and ONOO $^-$) can function as important physiological regulators of the intercellular signaling pathway in plant cells (Desikan et al. 2001; LiQiang 2011; Nie et al. 2006). However, they can cause disorders of oxidative phosphorylation due to oxidation and nitration of proteins. Anoxic and post-anoxic stresses by frequent flooding lead to ROS formation due to over-reduction of mETC, and these further lead to decreases in energy production (Blokhina and Fagerstedt 2010; Blokhina et al. 2000; Santosa et al. 2007; Szal et al. 2003). Under such stress conditions, non-phosphorylating components of mETC, the alternative oxidase (AOX) and type II NAD(P)H dehydrogenases (NDs) can consume the accumulated reducing equivalents for maintaining the mitochondrial homeostasis. These components are not coupled with the proton motive force (Blokhina et al. 2014; Maxwell et al. 1999; Millar et al. 2004; Møller 1997; Sweetlove et al. 2006; Szal et al. 2003; Xu et al. 2011) (Fig. 2). The AOX

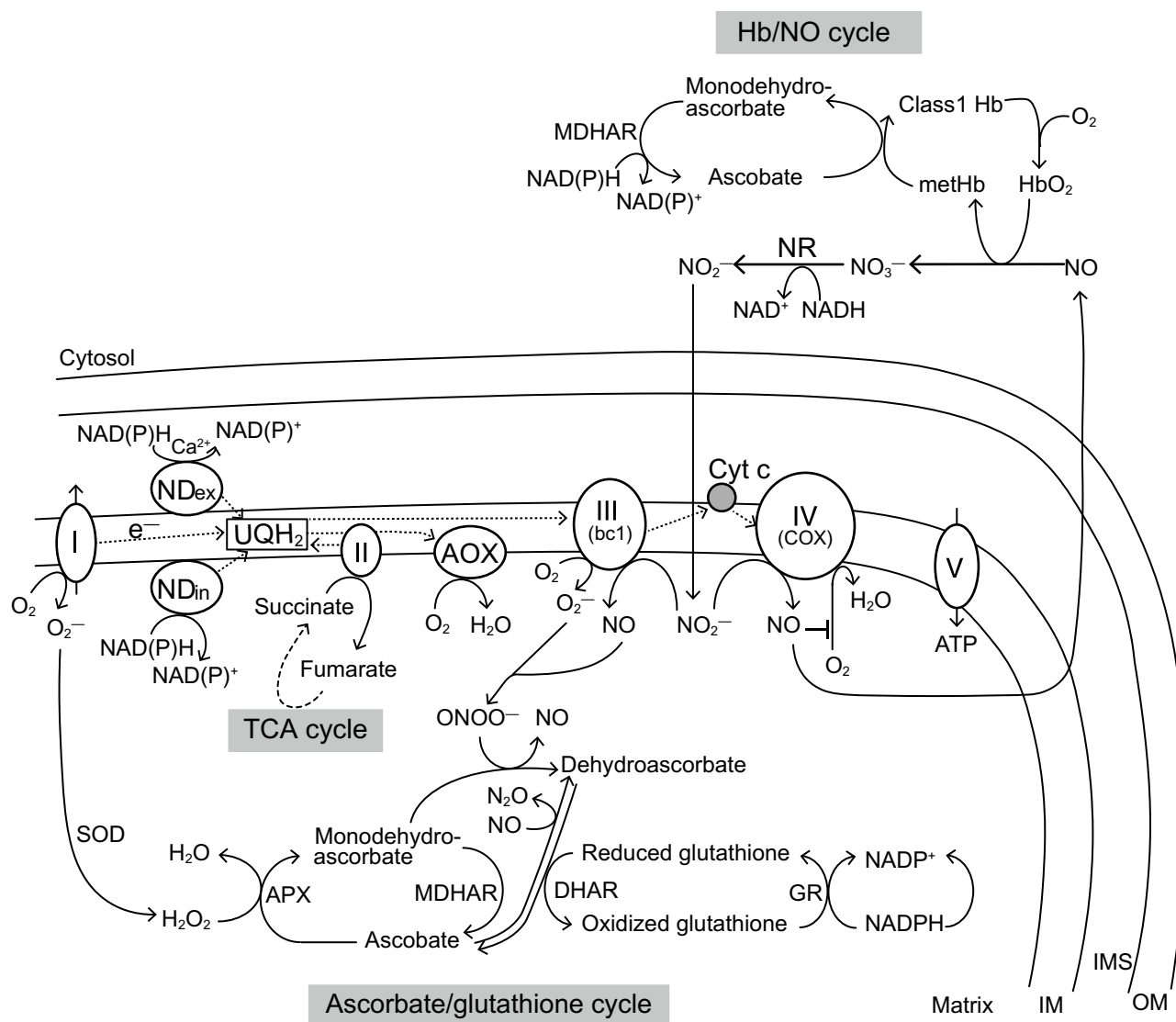


Fig. 2 Production and elimination of reactive oxygen species (ROS) and reactive nitrogen species (RNS) in mitochondria and cytosol. H_2O_2 , NO, O_2^- , and $ONOO^-$ produced under hypoxic stress conditions are detoxified by the mitochondrial electron transport chain (mETC) and ascorbate/glutathione cycle in the mitochondrial matrix to maintain a redox balance in the cells. The alternative oxidase (AOX) and type II NAD(P)H dehydrogenases (NDs), ND_{ex} , and ND_{in} (NDs located at the outer and inner surfaces of the mitochondrial inner membrane, respectively), can consume the accumulated reducing equivalents for maintaining the mitochondrial homeostasis. AOX has lower affinity to O_2 than cytochrome *c* oxidase (COX, complex IV); NDs, especially Ca^{2+} dependent ND_{in} , have lower affinity to NAD(P)H than complex I and nitrate reductase (NR). In NO scav-

enging under hypoxic stress condition, ascorbate can contribute to the reduction of NO to N_2O in the mitochondrial matrix. Ascorbate is converted to monodehydroascorbate by ascorbate peroxidase (APX), which also involves the scavenging of $ONOO^-$ and converting it into NO. The NO generated is resupplied to mETC. Ascorbate can also participate in Class 1 hemoglobin (Class 1 Hb) regeneration from methemoglobin (metHb) in the cytosol. Abbreviations are as follows: Cyt *c*, cytochrome *c*; DHAR, dehydroascorbate reductase; GR, glutathione reductase; IM, inner membrane; IMS, inter-membrane space; MDHAR, monodehydroascorbate reductase; NO, nitric oxide; NR, nitrate reductase; OM, outer membrane; SOD, superoxide dismutase; TCA, tricarboxylic acid; UQH_2 , ubiquinol

directly transfers an electron from ubiquinol (UQH_2) to O_2 , and functions in the stress response (Fig. 2). AOX has lower affinity for O_2 than cytochrome *c* oxidase (COX, complex IV) (Gupta et al. 2009), but O_2 consumption through AOX does not depend on O_2 concentration. In contrast, O_2 consumption through COX decreases depending on the decrease

in O_2 concentration (Zabalza et al. 2009). Thus, AOX can consume reducing equivalents under low O_2 conditions even when COX activity is inhibited. The AOX activity is controlled by its protein amount, AOX and ubiquinone (UQ) redox states, and pyruvate level (Day and Wiskich 1995; Møller 2001; Simons and Lambers 1999; Vanlerberghe and

McIntosh 1996; Vanlerberghe et al. 2002). A study in which the transcript responses to low O_2 between flood-tolerant rice and poplar and flood-intolerant Arabidopsis were compared revealed differences in the response of their AOX genes. The induction of AOX in response to low O_2 was observed in Arabidopsis but not in rice and poplar (Narsai et al. 2011). In the case of Arabidopsis, the expression of AOX gene is induced by citrate accumulation resulting from the inhibition of aconitase activity by NO formed under low O_2 stress. Consequently, the primary metabolism shifts to amino acid biosynthesis to counteract the energy crisis under low O_2 stress (Gupta et al. 2012). However, when O_2 availability is a limiting factor for the O_2 consumption, this AOX induction would be futile for O_2 consumption and energetically burdensome. Thus, the inability of Arabidopsis to prevent the induction of AOX genes under low O_2 conditions could be reasonable for its intolerance to anaerobic conditions (Shingaki-Wells et al. 2014). Interestingly, the *in vivo* AOX activity correlates with the relative growth rate in some wild species (Millenaar et al. 2001). It has been reported that AOX in illuminated leaves can contribute to optimizing the photosynthetic electron transport through the dissipation of excessive reducing equivalents under stress conditions, and the *AOX1* gene expression and AOX capacity are often induced by the presence of exogenous H_2O_2 or under stress conditions with high light or high temperatures (Amor et al. 2000; Feng et al. 2010; Murakami and Toriyama 2008; Vanlerberghe and McIntosh 1996; Vishwakarma et al. 2015; Wagner and Krab 1995; Xu et al. 2011). These results support that AOX is indispensable for the flexible control of ATP synthesis to maintain homeostasis and growth through the interaction between mitochondria and other organelles under various stress conditions (Hansen et al. 2002).

It has been reported that the induction of AOX is associated with the mitochondrial retrograde signaling and AOX can directly influence mitochondrial signaling by decreasing the ROS and uncoupling the electron transport from ATP synthesis (Rhoads and Subbaiah 2007). One of the TFs involving the AOX gene expression is related to abscisic acid (ABA), ABI4; it was reported to be a strong repressor of AOX expression in leaves of Arabidopsis exposed to high light and temperature stress (Giraud et al. 2009; Møller and Sweetlove 2010; Neill et al. 2003; Selinski et al. 2018; Xu et al. 2011). ABI4 is also intimately involved in sugar and plastid retrograde signaling pathways (Woodson and Chory 2008). Therefore, AOX could be controlled through ABI4 to integrate the mitochondrial retrograde signaling and respiratory regulation with other cellular anterograde and retrograde regulatory pathways. Vanlerberghe et al. (2009) indicated that AOX could buffer cellular signaling pathways, including cell death pathways, against adverse conditions. Moreover, AOX can regulate the gene expression of ROS-scavenging enzymes such as glutathione S-transferase,

catalase, ascorbate peroxidase (APX), and superoxide dismutase (Giraud et al. 2009; Rhoads and Subbaiah 2007). In many plants under post-anoxic conditions with high ROS production, the AOX induction was found at both the transcript and protein levels to support a rapid response to reoxygenation shock (Howell et al. 2007; Millar et al. 2004; Narsai et al. 2009).

Ca^{2+} -dependent NDs located at the outer (ND_{ex}) and inner (ND_{in}) surfaces of the mitochondrial inner membrane are not coupled with the generation of the proton motive force, and function as a bypass of complex I (Michalecka et al. 2003; Møller 1997; Rasmusson et al. 2004) (Fig. 2). The ND_{ex} can mainly utilize the cytosolic reducing equivalents (NAD(P)H) and have a higher K_m for NADH than those of complex I and nitrate reductase (NR) (Møller et al. 1993). As ND_{ex} can utilize NAD(P)H independently of the other processes of mETC, it can regulate the NAD(P)H levels inside the intermembrane space and cytosol (Igamberdiev and Hill 2004) (Fig. 2). Moreover, it can be regulated by the elevated concentration of cytosolic Ca^{2+} , due to Ca^{2+} release from the mitochondria during hypoxia (Fig. 2). An increase in the cytosolic Ca^{2+} concentration is stimulated by NO and H^+/Ca^{2+} antiport, which is linked to the decrease in the cytosolic pH (Igamberdiev and Kleczkowski 2003; Subbaiah et al. 1998). The increase in Ca^{2+} concentration under anaerobic conditions functions as a signal for the regulation of many enzymes such as GDC and NAD⁺ kinase (Igamberdiev and Hill 2008). Interestingly, *NDB2*, a gene encoding the ND_{ex} , is strongly co-expressed with *AOX1a* in Arabidopsis because these genes share many common cis-acting regulatory elements (CAREs) in their promoter regions and are affected in a similar manner (Clifton et al. 2005; Elhafez et al. 2006). Further, some of the NDs (*NDC1* and *NDA1*) are dual-targeted to plastids and peroxisome, therefore, their regulation is affected by the proteins outside the mitochondria (Ho et al. 2008). These indicate that important mitochondrial components involved in stress responses could provide the means for coordinating the activities between the organelles via coregulation and dual localization.

Effect of inorganic N sources on respiration in plants under the O_2 -deficient conditions

Plant roots play an important role in the absorption and assimilation of N and other essential minerals using respiratory energy. In soil, NO_3^- and NH_4^+ are found as inorganic N sources, and the energy cost for NH_4^+ assimilation is lower than that for NO_3^- (Bloom et al. 1992). Many terrestrial plants prefer to NO_3^- as inorganic N source, while wetland species specialize in NH_4^+ utilization because NH_4^+ predominates in flooded soils in their habitats. However, some wetland plants with the ability to supply O_2 from the shoots to the roots can utilize NO_3^- because active radial

O₂ loss (ROL) from their root tips allow nitrification in their rhizosphere (Brix et al. 2002; Kirk and Kronzucker 2005). The preference of the roots for inorganic N sources affects the ATP production levels and O₂ concentrations in roots. This is because the respiratory system has different responses to NO₃⁻ and NH₄⁺ under anaerobic conditions.

Two NO₃⁻ reduction pathways in plants under O₂-deficient conditions

Exogenous NO₃⁻ can act as a terminal acceptor of electrons and protons in the absence of molecular O₂. NO₃⁻ can accept reducing equivalents to regenerate NAD(P)⁺ and prevent deteriorative effects of the cytoplasmic acidification through assimilative or catabolic NO₃⁻-reduction pathways (Fig. 3, Fan et al. 1997; Müller et al. 1994; Vartapetian and Polyakova 1999). NAD(P)H can be oxidized by the assimilative pathway in which NO₃⁻ is reduced to NO₂⁻ and NH₄⁺, and by the catabolic pathway involving the reductive NO₂⁻-dependent NO production. These two pathways contribute to up-regulation of glycolysis under hypoxic and anoxic conditions due to the facilitation of glycolytic flux (Igamberdiev and Hill 2004; Reggiani et al. 1985; Stoimenova et al. 2007). Under low O₂ and acidic conditions, the transcript level and activity of NR, which catalyzes the first step of NO₃⁻ reduction to NO₂⁻ in both pathways, are increased in some terrestrial species (Lager et al. 2010). The NO₃⁻ reduction through the catabolic reduction pathway requires a large amount of NAD(P)H. In the NO₂⁻-driven ATP synthesis cycle, about 2.5 mol NADH per 1 mol NO₃⁻ is consumed. Thus, the flux to glycolytic fermentation decreases as a result of competition for NADH oxidation (Fan et al. 1988; Sowa et al. 1998).

In maize and barley roots, an increase in the NR activity under anaerobic conditions in the presence of NO₃⁻ was observed to be accompanied by a decrease in the ethanol accumulation (Botrel and Kaiser 1997; Fan et al. 1988). In contrast, in roots of rice and *Carex* species (*C. pseudocyperus* L. and *C. sylvatica* Huds.) under anaerobic conditions, exogenous NO₃⁻ stimulated anaerobic respiration (glycolytic fermentation) due to an accelerated glycolytic flux. This stimulation results from a more effective NADH reoxidation capacity by both NO₃⁻ reduction and fermentation compared with only fermentation (Müller et al. 1994; Reggiani et al. 1985, 1993). Moreover, high capacity to use NO₂⁻ as an electron acceptor strongly contributes to continuous ATP production in roots of rice and barley under anoxic stress (Stoimenova et al. 2007). This is because the NO₂⁻-driven ATP synthesis cycle is activated by the addition of NO₃⁻ under anoxic conditions (Fig. 3). These indicate that, under O₂-deficient conditions, NO₃⁻ has a favorable effect on the energy metabolism in roots of terrestrial as well as wetland plants.

The balance of the oxidation capacity of reducing equivalents (NADH) between the fermentation and the catabolic NO₃⁻-reduction pathways may be different among species (Fig. 3). The protective effects of NO₃⁻ utilization in rice shoots have been confirmed by analyzing their mitochondria using electron microscopy. In this study by Vartapetian et al. (2003), the marked destructive changes in the coleoptile mitochondria ultrastructure (membrane destruction, cristae disappearance, and pale matrix) were delayed until 48 h after the onset of anaerobic incubation in the presence of exogenous NO₃⁻. In rice plants, NO₃⁻ is reduced through the assimilative NO₃⁻-reduction pathway in their shoots because they show high activities and transcript levels of NR and GS when they are grown in both NO₃⁻ and NH₄⁺ conditions (Yun et al. 2008). In contrast, under O₂-deficient conditions, NO₃⁻ is reduced to NO₂⁻ by the catabolic NO₃⁻-reduction pathway in their roots. These reports imply that the capacities of the two NO₃⁻-reduction pathways, the assimilative and catabolic pathways, vary in the different tissues of a plant under anaerobic condition. Both pathways can contribute to hypoxic-stress tolerance through favorable effects on energy metabolism and cytoplasmic pH stabilization (Fig. 3).

NO₂⁻-driven ATP synthesis in plants under O₂-deficient conditions

Under O₂ deficient conditions, exogenous NO₃⁻ is reduced to NO₂⁻ by hypoxia-induced NR (Lager et al. 2010). When the O₂ level falls below the saturation level of COX, mETC utilizes NO₂⁻ as the electron acceptor instead of O₂ for the maintenance of ATP synthesis and O₂ concentration in cells (Gupta et al. 2005; Planchet et al. 2005) (Fig. 2). The rates of this NO₂⁻-driven anaerobic ATP synthesis are of the same order as those of glycolytic ATP production during hypoxia, and about 3–5% of the aerobic mitochondrial ATP synthesis (Stoimenova et al. 2007). As NO produced by this NO₂⁻-driven ATP synthesis is immediately converted to NO₃⁻ through the hypoxia-induced Class 1 hemoglobin (Class 1 Hb), mETC components including COX are not damaged (Gupta and Igamberdiev 2011; Nie et al. 2006; Taylor et al. 1994) (Fig. 2). The expression of Class 1 Hb gene is triggered by a disruption of ATP synthesis and by Ca²⁺ release under O₂-deficient conditions (Nie et al. 2006). Class 1 Hb has an extremely high affinity to O₂, and its oxidized form, oxyHb, can oxygenate NO to NO₃⁻ even at extremely low O₂ concentrations (Trevaskis et al. 1997) (Fig. 2). In such a case, homeostasis of O₂ and ROS is maintained because NO can tightly control respiration via inhibiting COX, which leads to an increase in the internal O₂ levels under hypoxic conditions (Gupta et al. 2014). Thereafter, NO₃⁻ is reduced to NO₂⁻ by hypoxia-induced NR and recycled by the operation of this Hb/NO cycle (Gupta and Igamberdiev 2011; Igamberdiev

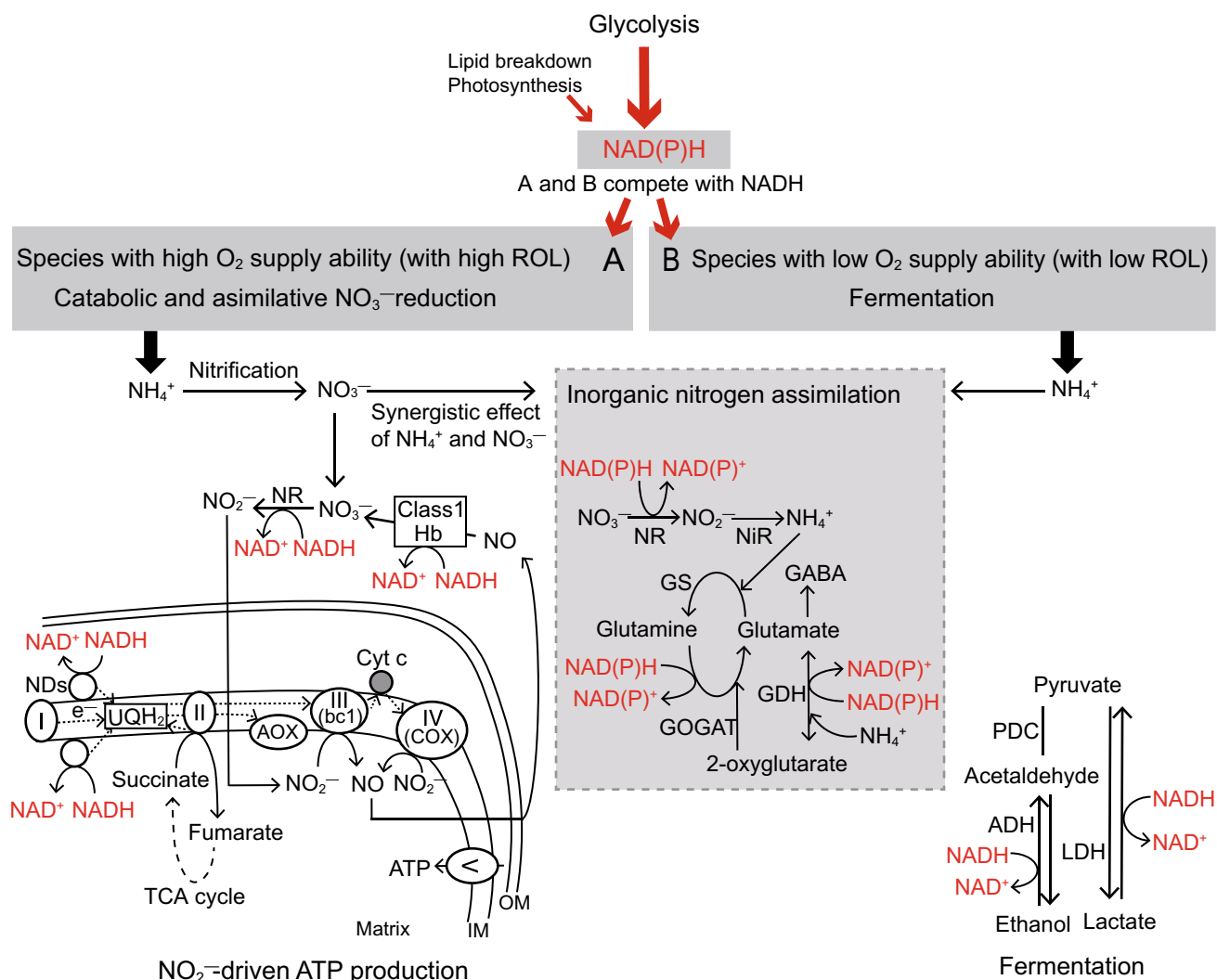


Fig. 3 Different utilization strategies of inorganic nitrogen (N) source for the maintenance of ATP production caused by the difference in the O₂ supply ability in wetland plants under O₂-deficient condition. NAD(P)H produced mainly during glycolysis, lipid breakdown, and photosynthesis is oxidized to NAD(P)⁺ by the following two pathways competing for the oxidation, assimilation, and catabolic reduction of NO₃⁻: NO₂⁻-driven ATP production (A) or fermentation (B). The oxidation of NAD(P)H is shown by red letters and arrows. (A) As the species with high O₂ supply ability can accelerate nitrification in their rhizosphere by high radial O₂ loss (ROL) from the roots, they can utilize NO₂⁻ produced from NO₃⁻ by hypoxia-induced nitrate reductase (NR) as the electron acceptor in the mitochondrial electron transport chain (mETC) instead of O₂. NO₂⁻-driven ATP production enables NAD(P)H oxidation for regulating glycolysis, avoiding cytosolic anoxia, and anaerobic ATP synthesis, which is in the same order as that in the ATP through fermentation during hypoxia. Moreover, species with high potential for NR can oxidize NAD(P)H for N assimilation, and these species can acquire a large amount of N and productivity by the “synergistic effect of NH₄⁺ and

NO₃⁻”. (B) The species with low O₂ supply ability specializing in the assimilation of NH₄⁺ that dominates the anaerobic soil may oxidize NAD(P)H through fermentation. NAD(P)H levels in the A and B pathway are regulated by glycolysis with pyrophosphate (PP_i) utilization by PP_i-dependent phosphofructokinase (PFK-PP_i) and pyruvate phosphate dikinase (PPDK) instead of ATP and metabolisms of major amino acids such as the alanine, glutamate, 2-oxoglutarate, and γ -aminobutyric acid (GABA). Thus, in wetland plants, A and B pathways function as the N utilization strategy in maintaining the ATP production under anaerobic conditions. Abbreviations are as follows: ADH, alcohol dehydrogenase; AOX, alternative oxidase; bc1, cytochrome bc₁; Class 1 Hb, class 1 hemoglobin; COX, cytochrome c oxidase; Cyt c, cytochrome c; GS, glutamine synthetase; GOGAT, glutamine oxoglutarate aminotransferase; GDH, glutamate dehydrogenase; IM, inner membrane; LDH, lactate dehydrogenase; NDs, mitochondrial NAD(P)H dehydrogenases; NiR, nitrite reductase; OM, outer membrane; PDC, pyruvate decarboxylase; TCA, tricarboxylic acid; UQH₂, ubiquinol, I–V; mitochondrial complexes I–V

and Hill 2004; Igamberdiev and Kleczkowski 2011). In the reaction when NO is converted to NO₃⁻, the heme iron of Hb is oxidized to its ferric form, methemoglobin (metHb)

(Fig. 2). To maintain the Hb/NO cycling, Class 1 Hb is regenerated from metHb by ascorbate (Fig. 2). The oxidized form of ascorbate, monodehydroascorbate, is reduced by

monodehydroascorbate reductase (MDHAR) along with the oxidation of NAD(P)H (Igamberdiev et al. 2006; Loreti et al. 2005) (Fig. 2). High ascorbate level and induction of MDHAR are observed under hypoxia (Igamberdiev et al. 2006). Besides playing a role in the above cycle, ascorbate also has an important role in the detoxification of ROS and RNS such as H_2O_2 , ONOO^- , and O_2^- . In the NO scavenging process under hypoxia, ascorbate reduces NO to N_2O in the mitochondrial matrix while monodehydroascorbate produced from ascorbate oxidizes ONOO^- to NO, and thus resupplies NO back to the cell (Alegría et al. 2004; Igamberdiev and Hill 2008) (Fig. 2). The Hb/NO cycling is influenced by the cytosolic NO_2^- accumulation via high NR activation. This NR activation is induced by the decrease in ATP during hypoxia/anoxia, but inhibited by low NO_3^- concentrations (Gupta et al. 2011; Planchet et al. 2005; Rockel et al. 2002; Stöhr and Mäck 2001). Thus, it seems that NO_2^- -driven ATP production may be an important strategy for hypoxia-tolerance in plants with high NR potential.

The turnover of NO and maintenance of the cellular redox and energy levels are strong evidence for NO_2^- -driven ATP production in some terrestrial plants, such as maize, alfalfa, and barley growing on NO_3^- dominant soils under low O_2 stress (Dordas et al. 2003; Igamberdiev and Hill 2004; Igamberdiev et al. 2006; Sowa et al. 1998). Moreover, NO_2^- -driven ATP production was also reported in rice plants that typically prefer NH_4^+ when exogenously supplied with NO_2^- and NO_3^- under anoxic conditions (Ohwaki et al. 2005; Stoimenova et al. 2007). The rate of anaerobic NO_2^- -driven mitochondrial ATP synthesis in rice was reported to be 25% of their total ATP turnover rate compared to that of 11.5% in barley during hypoxia (Stoimenova et al. 2007). These values were calculated based on the estimations that mitochondrial proteins represent 7% of the total proteins in heterotrophic plant cells (Douce 1985) and the rate of ATP turnover is $70 \text{ nmol min}^{-1} \text{ mg}^{-1}$ mitochondrial protein (Neuburger et al. 1996). This rate could be much higher in rice, 35% of the total ATP turnover rate, because the mitochondrial proteins of rice could comprise as much as 10% of the total proteins (Stoimenova et al. 2007). The ATP production per anaerobic mitochondrial NAD(P)H oxidation of rice is also higher than that of barley (Stoimenova et al. 2007). Thus, species that possess high potential of NO_2^- -driven ATP production system and contain abundant mitochondrial proteins such as rice plants, can increase their ATP production per anaerobic mitochondrial NAD(P)H oxidation when they utilize NO_3^- as the N source. So far, the contribution of NO_2^- -driven ATP production system in wild wetland plants has been unnoticed because these plants prefer NH_4^+ in their habitats as nitrification is restricted by stagnant water. However, this system could become a crucial strategy in hypoxia-tolerant wild wetland species

with a high ATP turnover rate, when NO_3^- is available in their rhizosphere.

Differences in effects of NH_4^+ on respiration between terrestrial and wetland plants

The energy cost for NH_4^+ assimilation is lower than that for NO_3^- (Bloom et al. 1992). However, many terrestrial plants need to assimilate NH_4^+ immediately after their absorption in the roots to avoid the toxicity symptoms associated with NH_4^+ as the sole N source (Britto and Kronzucker 2002). Concentrated NH_4^+ often increases the respiration rate (NH_4^+ -dependent respiratory increase, ARI) in shoots, roots, and whole plants (Britto et al. 2001; Escobar et al. 2006; Hachiya et al. 2010). Thus, NH_4^+ utilization may lead to further O_2 deficiency through ARI in many terrestrial plants when the N source is limited to only NH_4^+ by rhizosphere environmental changes such as submergence. In shoots and roots of terrestrial plants, ARI that is induced by an increase in NH_4^+ concentration in the external media (Britto et al. 2001) increases the ATP content and ATP/ADP ratio by inducing the phosphorylating components of mETC such as complex I, III, and IV (COX) (Curi et al. 2003; Hachiya et al. 2010; Welchen et al. 2002). However, these increases in respiratory ATP production are not related to an increase in useful energy demands such as growth. One of the main causes of ARI has been suggested to be an increase in the inward/outward flux of NH_4^+ across the plasma membrane, called “futile NH_4^+ cycling (FAC)” (Britto and Kronzucker 2002; Britto et al. 2001; Hachiya et al. 2010). As NH_4^+ uptake via the NH_4^+ transporter (AMT) is accompanied by proton extrusion from the plasma membrane H^+ -ATPase to maintain the cytosolic charge balance (Britto and Kronzucker 2002), the increased FAC under conditions of NH_4^+ as the sole N source would require more respiratory ATP (Britto et al. 2001). Consequently, ARI would occur to meet the increase in ATP demand related to increased FAC, when the plants are grown under high concentration of NH_4^+ . Indeed, in some NH_4^+ -intolerant terrestrial species such as maize and barley, the H^+ -ATPase activity is high when they are grown under conditions of NH_4^+ as the sole N source (Britto et al. 2001; Nielsen and Schjoerring 1998; Schubert and Yan 1997). In contrast, in the roots of NH_4^+ -tolerant rice, ARI is not observed (Britto et al. 2001), and the activity of H^+ -ATPase is independent of the N source (Zhu et al. 2009). Moreover, the experiments in which NH_4^+ metabolism and growth rate are analyzed in rice plants have reported that the decrease in energy cost for FAC does not correlate with the optimized growth (Balkos et al. 2010). This low FAC in rice plants may reflect that they have evolved to be NH_4^+ tolerant without any energy cost to maintain the NH_4^+ balance across the plasma membrane (Karasawa et al. 1994; Kronzucker et al. 1999, 2001).

ARI is also explained by another hypothesis in which it occurs in relation to the dissipation of excess reducing equivalents in mETC. The NO_3^- assimilation process competes with mETC for the reducing equivalents. The shift of an available N source from NO_3^- to NH_4^+ increases the reducing equivalents that are not consumed through NO_3^- assimilation and are thus available to be consumed by mETC, thereby increasing the O_2 uptake rate (Bloom et al. 1992; Escobar et al. 2006). In particular, under low O_2 stress conditions where COX is saturated with reducing equivalents, there is a possibility that the non-phosphorylating AOX and NDs in mETC can consume the excessive reducing equivalents without being limited by adenylate control (Escobar et al. 2006; Vanlerberghe et al. 2009). In fact, AOX capacity in terrestrial plants such as Arabidopsis, pea, and spinach increases when they are transferred from NO_3^- to NH_4^+ conditions (Escobar et al. 2006; Frechilla et al. 2002; Lasa et al. 2002). NDB2, which is a major isoform of ND_{ex} , is also induced in shoots and roots of Arabidopsis under NO_3^- -depleted conditions (Wang et al. 2004; Watanabe et al. 2010). Although these responses have an important role in the dissipation of excessive reducing equivalents under the low O_2 stress conditions, ARI itself would lead to further strict anoxic threat for NO_3^- -preferring terrestrial plants under O_2 -deficient condition.

Two contrasting adaptive strategies in flood-tolerant plants: the low oxygen escape strategy versus the low oxygen quiescence strategy

Flood tolerant plants that can survive at O_2 deficiency or light-limited submergence conditions are characterized by two survival strategies. One of them is the low O_2 escape strategy (LOES), and the other is the low O_2 quiescence strategy (LOQS) (Fig. 4). Plants with LOES phenotypes show upward bending of leaves (hyponasty) that can enhance shoot elongation, formation of interconnected air-filled voids (aerenchyma), induction of barriers to radial O_2 loss (ROL) in roots, development of adventitious roots (ARs), formation of gas films on leaf surfaces, modification in leaf anatomy, and pressurized gas flow through porous tissues under O_2 -deficient conditions. All of these characteristics are not necessarily found in one species (Blom 1999; Evans 2004; Jackson and Armstrong 1999; Ridge 1987; Sauter 2013) (Fig. 4). The elongation of aerial organs and the formation of aerenchyma and ARs are all ethylene dependent. The former trait is also controlled by a hormonal network, which includes ABA and GA, and the latter trait by ROS (Voisenek and Bailey-Serres 2015) (Fig. 4). In contrast, plants with LOQS phenotypes cease their growth and save their carbohydrate reserves under O_2 -deficient conditions.

Molecular mechanisms of LOES and LOQS

In rice varieties, both LOES and LOQS are found to counteract flooding stress. *SNORKEL1* (*SK1*) and *SNORKEL2* (*SK2*) of deep-water rice varieties (LOES type) are involved in the rapid internode elongation and escape of leaves near the water surface (Hattori et al. 2009), whereas *submergence 1A-1* (*SUBIA-1*) in lowland varieties of rice (*indica*) (LOQS type) limits elongation, growth, and carbohydrate consumption (Fukao and Bailey-Serres 2008; Fukao et al. 2006) (Fig. 3). The key regulatory genes in both strategic responses are the ethylene-responsive TFs of the subfamily group VII (ERF-VII); the TFs act downstream of ethylene and modulate GA-mediated shoot growth (Bailey-Serres and Voisenek 2010; Voisenek and Bailey-Serres 2015). Deepwater varieties of rice (LOES type) can escape from adverse partially submerged deep-water conditions through *SK1* and *SK2* genes (*SKs*) that trigger rapid internode elongation at a rate of 25 cm day^{-1} (Colmer et al. 2014; Hattori et al. 2011) (Fig. 4). In contrast, these genes are absent in shallow water varieties including all *japonica* varieties (LOQS type). Moreover, two additional uncharacterized loci on chromosomes 1 and 3 (*QTL1* and 3) are needed along with *SKs* for the full deep-water escape response (LOES type) (Ayano et al. 2014). Shoot and internode elongations in submerged deep-water varieties of rice are promoted by cell expansion and division, which are positively regulated by ethylene and GA (GA_1 and GA_4). These hormones enable expansins (EXPs) and α -amylase to drive cell elongation and starch degradation by *SKs* and *QTL1* and 3 (Choi et al. 2004; Rzewuski and Sauter 2002; Sauter et al. 2002; van der Knaap et al. 2000) (Fig. 4).

In contrast, the *indica* varieties possessing *SUBIA-1* (LOQS type) decrease their metabolic activities and constrain their growth to save energy consumption under shortly prolonged submergence conditions (up to only a few weeks) (Fig. 4). The *indica* and *japonica* varieties lacking the *SUBIA* gene or *SUBIA-1* allele cannot cease their metabolic activities (Fukao et al. 2006; Xu et al. 2006). *Submergence 1* (*SUB1*) locus of rice consists of three genes, *SUBIA*, *SUBIB*, and *SUBIC*. The expression of *SUBIA-1* alone is sufficient to provide flood tolerance, but it exists only in flood-tolerant varieties with LOQS traits. *SUBIC* is present in all varieties, and responds to GA and positively regulates the expression of several EXPs (Fukao and Bailey-Serres 2008; Hattori et al. 2011; Xu et al. 2011). *SUBIB* is ERF similar to *SUBIC* (Bailey-Serres et al. 2010). The submergence-intolerant *japonica* cultivar Nipponbare has both *SUBIB* and *SUBIC*, but lacks *SUBIA*. *SUBIA-1* inhibits shoot elongation by maintaining the levels of TFs, SLENDER RICE 1 (SLR1) and SLENDER RICE-Like 1 (SLRL1), to counterbalance the GA responsiveness and regulate the *SUBIC* mRNA level negatively (Bailey-Serres

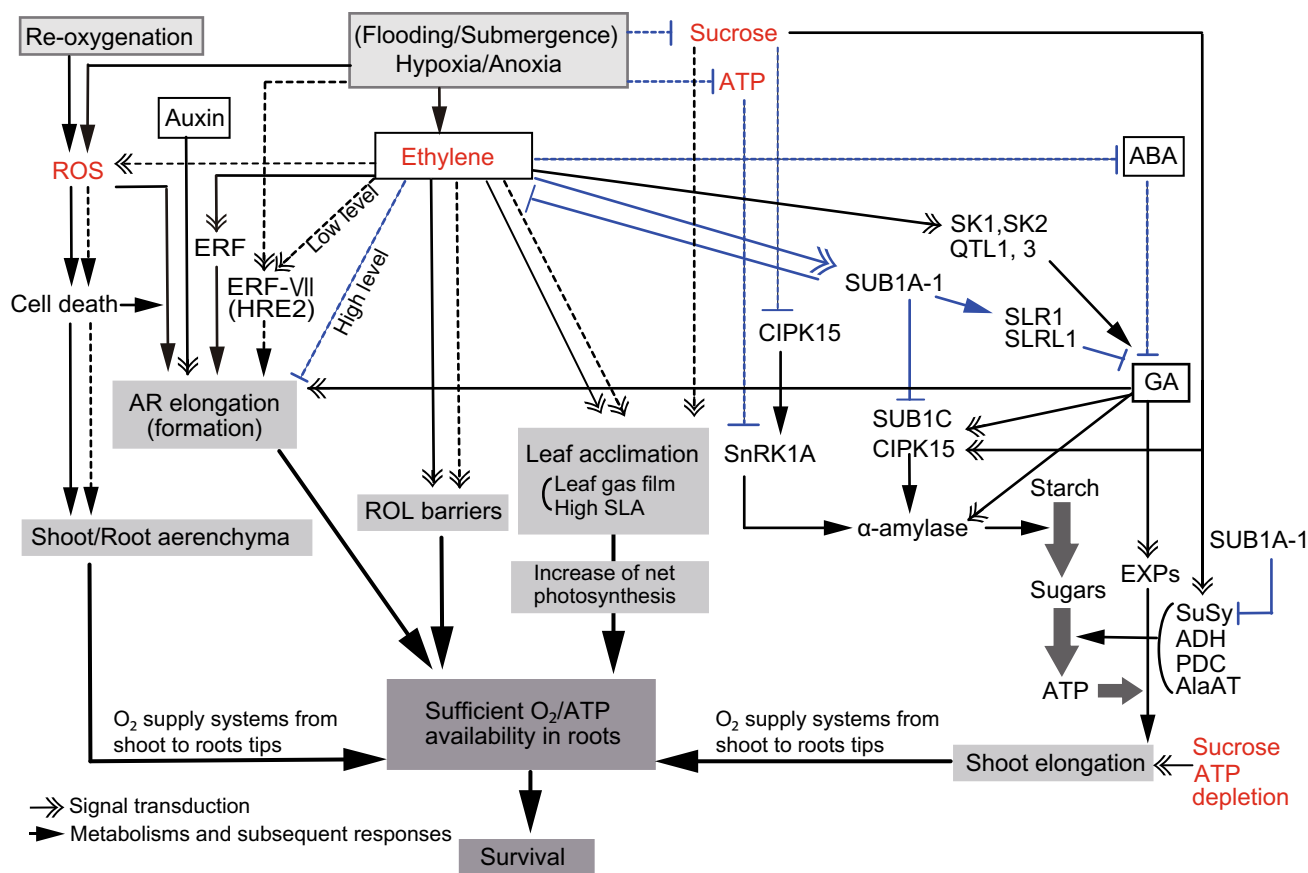


Fig. 4 Characteristics of low O₂ escape strategy (LOES) and low O₂ quiescence strategy (LOQS) to hypoxia/anoxia caused by flooding/submergence in wetland and terrestrial plants. Black solid and dashed lines are the networks of LOES (aerenchyma formation, shoot elongation, radial O₂ loss (ROL) barriers, and leaf acclimation) in wetland and terrestrial plants, respectively, while blue dashed lines indicate responses to suppress LOES in both plants; blue solid lines indicate the submerged regulatory network of LOQS in rice (wetland species). Four key factors, ROS accumulation, ethylene content, ATP depletion, and sucrose reserve decrease, involve the LOES and LOQS networks are shown in red letters. ROS production in hypoxic and anoxic stresses causes programmed cell death (PCD) in both plant types and involves the mechanisms of adventitious roots (ARs) emergence and aerenchyma formation. AR elongation in Arabidopsis (terrestrial plant) is promoted by the hypoxia signal and its formation is mediated by hypoxia-responsive HRE2, which is one of the group VII ethylene response transcription factors (ERFVIIIs). High ethylene level inhibits the AR formation in Arabidopsis under hypoxic condition, although ARs are formed at low ethylene level. In contrast, in rice plants, ethylene has promotive effects on the AR formation and elongation. The contrasting regulation by ethylene on ARs may reflect different adaptive strategies in the flood-tolerant rice plants compared to the flooding-intolerant terrestrial species such as Arabidopsis. Leaf acclimation such as high specific leaf area (SLA), reoriented chloroplasts along with cell wall in leaf epidermis, thin cuticles and cell walls, development of dissected leaves underwater,

and the maintenance of gas films can increase the net photosynthesis by decreasing the diffusion resistance for CO₂. The leaf plasticity could also result from the accumulation of ethylene and a decrease in CO₂ levels. Flooding/submergence causes ethylene accumulation, which triggers gibberellin (GA)-promoted cell elongation through the expansins (EXPs). In deep-water rice with LOES, ethylene promotes the induction of SNORKELS (*SKs*, *SK1*, and *SK2*) and GA elevation and the internodes of the shoots elongate rapidly to come out of the water surface. In the deep submergence lines of rice with LOQS, ethylene activates the submergence 1A-1 (*SUB1A-1*) promoting an increase in SLENDER RICE 1 (*SLR1*) and SLENDER RICE-Like 1 (*SLRL1*) transcription factors, which inhibit GA-mediated activation of gene expressions. This LOQS characteristic of rice can limit carbohydrate consumption by inhibiting shoot growth. Wetland plants develop shoot and root aerenchyma, ROL barriers, and elongated shoots elongation and these characteristics of LOES act synergistically with each other in enhancing the stability of O₂ and ATP availability in roots where nitrogen (N) uptake and active N assimilation take place. Abbreviations are as follows: ABA, abscisic acid; ADH, alcohol dehydrogenase; AlaAT, alanine aminotransferase; CIPK15, calcineurin B-like interacting protein kinase 15; HRE2, hypoxia-responsive ERF 2; PDC, pyruvate decarboxylase; *QTL1* and 3, quantitative trait loci on chromosomes 1 and 3; SnRK1A, sucrose non-fermenting receptor kinase 1A; SuSy, sucrose synthase; *SUB1A-1*, submergence 1A-1

and Voesenek 2008; Fukao et al. 2006) (Fig. 4). Furthermore, *SUB1A-1* negatively regulates the submergence-induced synthesis of ethylene, mRNA expression of

cell-wall-loosening EXP, starch and sucrose degradation (Fukao et al. 2006), and chlorophyll degradation through zinc-finger TF encoded by DELAY OF THE ONSET OF

SENESCENCE (Fukao et al. 2012; Winkel et al. 2014). The elongation processes through *SUBIC* require a large amount of energy during shoot submergence because elongation of aerial organs is accompanied with the rapid and efficient translocation of photosynthates and reserved carbohydrates and amino acids (Ayano et al. 2014; Hattori et al. 2011; Kende et al. 1998; Sauter 2000). In contrast, LOQS varieties with *SUBIA-1* can decrease their energy utilization until the water level decreases and normoxic conditions are restored, thereby they resume growth with preserved energy under subsequently normoxic conditions (Ayano et al. 2014; Barding et al. 2012, 2013; Fukao and Bailey-Serres 2008; Hattori et al. 2011; Kende et al. 1998; Nagai et al. 2010; Sauter 2000). The rice varieties with *SUBIA-1* can restrict the rate and extent of starch hydrolysis and accumulate lower concentrations of ethanol, lactate, and amino acids than the varieties without *SUBIA* (Barding et al. 2012, 2013). It has been assumed that repeated elongation of aerial tissues in every short-term submersion may damage the growth by serious re-oxidation and water loss in the LOQS phenotypes (Hattori et al. 2011; Nagai et al. 2010). The varieties with *SUB1* can manage ROS accumulation and leaf water loss during recovery from submergence conditions to a minimum extent. This is because they have higher levels of mRNA associated with the repression of ROS accumulation during the recovery phase (Fukao et al. 2011; Mustroph et al. 2010).

In wild wetland plants such as *Rumex palustris*, *R. acetosa*, *Sagittaria trifolia* and *Lotus tenuis*, it has been suggested that there are networks in conserved flooding response that relate to growth and stress-induced catabolism of carbohydrates for the efficient ATP production. However, studies on ERF-VII TFs (*SKs* and *SUB1*) are required in wild wetland species that experience long-term flooding (Kim et al. 2000; Manzur et al. 2009; Ookawara et al. 2005; Vreeburg et al. 2005). In these plants, there are considerable genetic variations between and within species in the ethylene-induced elongation capacity under submergence conditions. It is noteworthy that the wild species *R. palustris* displays submergence escape by ethylene-driven shoot elongation (LOES type) (Benschop et al. 2005), and *R. acetosa* invokes quiescence owing to a lack of ABA down-regulation, GA up-regulation, and increased EXP expression (LOQS type), although these two species are closely related to each other (Benschop et al. 2005; Chen et al. 2009; van Veen et al. 2013; Vriezen et al. 2000). In *R. palustris*, it seems that the elements downstream of ethylene and upstream of ABA and GA can switch on this elongation cascade (Benschop et al. 2005; Chen et al. 2009; van Veen et al. 2013). Moreover, *R. palustris* exposed to dark under submergence conditions can convert their strategy from escape to quiescence for survival. This strategy is achieved by the pretreatment using ethylene, in which LOQS ability is promoted (van Veen et al. 2013). This strategy conversion in *R. palustris* relates to

the light-signaling genes that regulate the enhancement of shoot elongation (van Veen et al. 2013), and this observation demonstrates the similarity of growth control between shade avoidance and underwater elongation. Another wetland species, *L. tenuis*, also elongates upon partial submergence but arrests its growth upon complete submergence. It switches from LOES to LOQS due to elevation of shoot porosity and limited consumption of soluble carbohydrates in shoots and roots (Manzur et al. 2009). Both antithetical LOES and LOQS strategies exist within a single species and are not mutually exclusive. These may be combined by the threshold of O₂ level or energy deficiency. In this regard, Voeselek and Bailey-Serres (2015) indicate that three key factors, an increase of cellular ethylene content, depletion of ATP, and consumption of readily available sucrose in the submergence network, can contribute to increased induction and regulation of shoot elongation. The level of reserved carbohydrates for ATP production seems to strongly affect the strategies for sustainable and facilitative survival in various natural flooding environments (Fig. 4). Especially the LOES type may be required for the high photosynthetic capacity and translocation activity of photosynthates and reserves under submergence conditions. Therefore, the interplay among hormones (ethylene, ABA, and GA), O₂ availability, and specific metabolites (ATP, sugars, and pyruvate) needs further clarification for understanding the network balancing growth and quiescence.

Avoidance strategies in LOES-type plants for improvement of O₂ level within plant tissues

When plants are submerged by flooding, species with LOES phenotypes respond to O₂ deficiency for improvement of cellular O₂ level. Shoot elongation, formation of interconnected air-filled voids (aerenchyma), pressurized gas flow through the aerenchyma and leaf acclimations for the decrease of the diffusion resistance to air can function to improve cellular O₂ levels. In the roots, developed aerenchyma, formation of the ROL barrier from the roots surface and development of ARs can enhance the longitudinal O₂ diffusion in root tips with the most active cells.

Aerenchyma Aerenchyma can decrease the gas diffusion resistance from the atmospheric tissues to the O₂-deficient tissues. The formation of aerenchyma and enhancement of the gas transport ability are essential strategies in LOES (Fig. 4). O₂ produced during photosynthesis or taken up by the aerobic shoots diffuses inside the aerenchyma connecting the shoots and the roots; this O₂ diffusion supports respiration in O₂-deficient underwater organs (Fig. 4). Aerenchyma can be formed by different processes such as schizogeny and lysigeny (Drew et al. 2000; Evans 2004; Seago et al. 2005). These processes often appear simultaneously

at different organs in one individual plant (Steffens et al. 2011). Although little is known about the process of schizogenous aerenchyma formation (Evans 2004), it has been hypothesized that the causal protein, NOPI, regulates the schizogenous formation of air chambers via a membrane-localized receptor-like kinase signaling pathway resulting in ubiquitylation and degradation of target proteins (Ishizaki et al. 2013). In contrast, the lysigenous formation of air chambers via programmed cell death (PCD) requires ethylene, Ca^{2+} , and ROS signaling, which ultimately breaks down the cell walls as observed in some species such as rice, *Arabidopsis*, maize, and wheat (Drew et al. 2000; Evans 2004). In roots of maize and deep-water rice, studies have reported that aerenchyma formation is associated with the accumulation of ROS and down-regulation of *METALLOTHIONEIN 2b* mRNA encoding a ROS scavenging protein (Rajhi et al. 2011; Steffens et al. 2011). Moreover, it seems that the Ca^{2+} -dependent plasma membrane-localized respiratory burst oxidase homologs (*RBOHs*) influence the ROS sources in this process as they have been reported to promote apoplastic superoxide production to amplify ROS-mediated signaling in wheat and rice (Parlanti et al. 2011; Yamauchi et al. 2013b).

Pressurized flow-through system In addition to the inward diffusion, a mechanism of gas transport in all wetland plants, some floating plants and macrophytes have a pressurized flow-through system in stems and rhizomes to aerate the O_2 -deficient underwater organs (roots and rhizome). This system enables the underwater organs to keep the O_2 concentration to an ambient level for maintaining oxidative phosphorylation, thereby normalizing the ATP concentration (Colmer 2003; Sorrell and Hawes 2009) (Fig. 4). Pressurized flow-through is produced by the species-specific positive pressure capacity in shoot tissues and the resistance to the flow in the aerenchyma. Also, leaf-to-air gradients of temperature and humidity affect the pressurized flow (Brix et al. 1992; Colmer 2003). This flow mechanism also contributes to an outward diffusion of ethylene generated in roots and methane generated in soils (Colmer 2003; Laanbroek 2009). Thus, pressurized flow-through that facilitates effective gas flow through developed aerenchyma seems to provide a competitive advantage to large varieties of plants in deep-water habitats (Konnerup et al. 2011).

Leaf acclimation In terrestrial plants, the net photosynthesis of submerged leaves often decreases significantly compared with that of aerial leaves due to an exponential decrease in light intensity with increasing depth and resistance to CO_2 and O_2 fluxes in submerged leaves (Colmer et al. 2011; Herrera 2013). In response to submergence, some terrestrial plants develop new acclimated leaves that are characterized by higher specific leaf area (SLA) that is a ratio of leaf area

to leaf mass, reoriented chloroplasts along with cell walls in leaf epidermis, thin cuticles and cell walls, development of dissections, and maintenance of gas films (Colmer et al. 2011; Mommer et al. 2005b) (Fig. 4). All of these traits can decrease the diffusion resistance to CO_2 , thereby enabling the leaves to increase the net rate of CO_2 assimilation and decrease the CO_2 compensation point under water (Mommer et al. 2006; Pedersen et al. 2013; Winkel et al. 2014).

Wetland plants, such as *Rumex palustris*, *R. acetosa* and rice, show plastic acclimation of their morphological, anatomical, and biochemical traits of leaves to submergence (Mommer et al. 2005a, b; Pedersen et al. 2009, 2013; Winkel et al. 2014). *Ranunculus repens* constitutively dissect their leaves when they grow underwater (He et al. 1999). In *R. palustris*, the new acclimating leaves developed in underwater conditions can lead to a nearly 40-fold decrease in the diffusion resistance to CO_2 (Mommer et al. 2005a). Rice plants show a large variation in these leaf traits among varieties. Submergence-tolerant landrace FR13A with LOES has higher net underwater photosynthesis, longer retention of the leaf gas film and longer persistence compared with a Sub1 variety, Swarna-Sub1 (Winkel et al. 2014; Xu et al. 2006). These traits of FR13A contribute to submergence tolerance because the persistence of gas film could potentially increase net photosynthesis and internal aeration during submergence. In contrast, in Swarna-Sub1, the duration of gas film retention is shorter than that in FR13A, although Swarna-Sub1 can maintain carbohydrate levels during submergence. Since both varieties have *SUB1A*, genetic determinants other than *SUB1A* contribute to gas film formation and underwater photosynthesis. Leaf acclimation ability to submergence may be related to flood tolerance in wetland plants with LOES. In contrast, these acclimations may not be related to flood tolerance in terrestrial plants (Mommer et al. 2007). The accumulated ethylene does not necessarily function as a signal for the flood-induced leaf acclimation in terrestrial plants under flooded conditions, but other signals associated with changed photosynthetic rates and/or decreased levels of carbohydrates may induce these leaf acclimations (Bailey-Serres and Voesenek 2008) (Fig. 4).

Barrier to radial O_2 loss The O_2 supplied from the above-ground to underground organs diffuses to the anaerobic soil as radial O_2 loss (ROL), which contributes to protecting the roots from toxic ions (Fe^{2+} and Mn^{2+}) and to the nitrification in NH_4^+ -predominant and excessive-reduced soils by the oxidized layers around the roots. Moreover, wetland plants and some terrestrial plants form an impermeable barrier to ROL from the root basal zone to the apex (ROL barrier) by the deposition of suberin in the root exodermis (Fig. 4). The suberin layer is mainly composed of long-chain fatty acids. The ROL barrier acts synergistically to enhance the longitudinal O_2 diffusion in the root tips with the most active cells

and enables the development of aerobic rhizosphere around the root tips for root extension (Abiko et al. 2012; Armstrong and Beckett 1987; Colmer 2003; Sauter 2013) (Fig. 4). The ROL barrier is permanently formed in some wetland species, or temporarily induced by waterlogging in rice and wheat (Colmer 2003; Kotula et al. 2009; Malik et al. 2011) (Fig. 4). Molecular investigations in rice plants have clarified that the ROL barrier formation involves the up-regulation of genes including a hypodermal cell ABC transporter (*REDUCED CULM NUMBER1* [*RCN1*]/*OsABCG5*), which is proposed to export the long-chain fatty acids and/or their derivatives across the hypodermal plasma membrane into the apoplast to induce hypodermal suberization (Shiono et al. 2014). Indeed, the metabolite profile analysis in rice roots growing under barrier-forming stagnant conditions reveals that the concentrations of long-chain fatty acids and malate, which is a substrate for fatty acid biosynthesis, gradually increase from the root apex to the base (Kulichikhin et al. 2014).

Adventitious roots Adventitious roots (ARs) are also associated with conferring developmental plasticity to plants under waterlogged condition. ARs with high porosities emerge from submerged stem nodes and hypocotyls to replace the existing and deteriorating primary root system in rice, *R. palustris*, *Solanum lycopersicum*, and *Larix laricina* (Calvo-Polanco et al. 2012; Dawood et al. 2014; Dawood et al. 2016; Eysholdt-Derzsó and Sauter 2019; Visser et al. 1996; Yang et al. 2018; Zhang et al. 2017) (Fig. 4). Some ARs develop chloroplasts and thus provide an additional source of O₂ and carbohydrates (Rich et al. 2012) because ARs typically develop in well-aerated topsoil layers (Dawood et al. 2014; Eysholdt-Derzsó and Sauter 2019; Zhang et al. 2015). The terrestrial plant *Solanum dulcamara* can survive under flooding condition by replacing the original flood-sensitive root system with aerenchymatous ARs that are produced from pre-formed primordia on the stem. The AR outgrowth is involved with auxins, ABA, and jasmonic acid (Dawood et al. 2016; Vidoz et al. 2010; Yang et al. 2018). ABA is a negative regulator of AR outgrowth, but there is a highly tissue-specific response to decreased ABA levels. Auxins may be necessary for AR outgrowth because a disruption in the auxin signaling in AR primordia of *S. dulcamara* resulted in the abortion of AR outgrowth under complete submergence (Dawood et al. 2016) (Fig. 4). Moreover, the auxin pathways act together with decreased levels of ABA because the AR emergence in *S. dulcamara* was not sufficient when they were treated with auxin alone (Yang et al. 2018).

In Arabidopsis, low levels of ethylene and hypoxia signals mainly promote AR elongation due to the expression of the hypoxia-responsive *HRE2* which is one of the ERFVII TFs (Bailey-Serres et al. 2012; Eysholdt-Derzsó and Sauter

2019; Hess et al. 2011) (Fig. 4). However, high levels of ethylene inhibit the initial formation of ARs because high ethylene concentration can override the hypoxia signal (Eysholdt-Derzsó and Sauter 2019). Thus, the formation and elongation of ARs in Arabidopsis are controlled by ethylene in a dose-dependent manner (Fig. 4). Although low levels of ethylene in Arabidopsis may contribute to fast elongation of ARs immediately after exposure to hypoxia, they cannot exert hypoxia tolerance. This is because they do not form subsequent ARs when exposed to long-term severe anaerobic stress associated with high ethylene accumulation. In contrast to Arabidopsis, ethylene has promotive effects on the AR emergence and growth in several wetland species including rice (Lin and Sauter 2018). The contrasting regulation of ethylene on ARs may reflect the different adaptive strategies between the flood-tolerant and intolerant species (Fig. 4).

The roles of these phytohormones in the terrestrial species would be different from those in rice plants, especially in the AR emergence pathway. The emergence of the AR primordia in rice plants involves PCD in the overlying epidermal cells, which is mediated by ethylene-promoted ROS production (Steffens et al. 2013) (Fig. 4). The developmental process of ARs involves the up-regulation of the plasma membrane *RBOHs* (Steffens et al. 2012), and the decrease in *METALLOTHIONEIN 2b*, which regulates the ROS amelioration for nodal AR emergence (Voesenek and Bailey-Serres 2015). The location of this PCD is determined by the force exerted by the outgrowing meristems, and at the same place, epidermal weakening for emergence of AR primordium can be elicited by the essential degradation of pericycle and epidermal cells by cell wall-modifying proteins such as EXPs, subtilisin-like proteases, pectate lyases, and endo- β -1,4-glucanases (Cho and Kende 1997; Kimpara et al. 2008; Laskowski et al. 2006; Steffens et al. 2012; Yamauchi et al. 2013a).

Diverse strategies for avoidance from O₂ deficiency In rice and some wetland species, ROL barrier and leaf acclimation improve their underwater photosynthesis, root aeration, and growth (Colmer and Pedersen 2008; Pedersen et al. 2009; Winkel et al. 2013, 2014) (Fig. 4). These characteristics act synergistically with each other to enhance flood tolerance in wetland species (Fig. 4). In contrast, acclimated leaves with morphological modifications and ARs cannot provide flooding tolerance to terrestrial plants because O₂ cannot be transported to the underwater organs of terrestrial plants (Fig. 4). As roots consume large amounts of O₂ for nutrient uptake, they often suffer from O₂ deficiency. The internal O₂ pressure in roots is much lower than that in shoots, especially at night when photosynthetic O₂ production ceases (Pedersen et al. 2006). Therefore, effective aerenchyma is required to enable the roots to sustain the oxidative phos-

phorylation leading to normal ATP production and growth (Visser and Pierik 2007). However, despite the benefits of aerenchyma under flooded conditions, it is not constitutive in all plants. In this regard, Striker et al. (2007) described the significant trade-off between root porosity and mechanical strength. Hu et al. (2013) also confirmed that aerenchyma inhibits radial nutrient transport in maize roots. Therefore, it could be assumed that many wetland plants can maintain an optimal balance between their growth and low O_2 tolerance in their roots, and this balance is significantly different from that in the terrestrial plants.

Traits of root N use and O_2 uptake in LOES-type wetland plants under O_2 -deficient conditions

Differences in the rhizosphere N conditions such as sole or mixture of NO_3^- and NH_4^+ generally change root density, extension, and whole weight. These changes alter the rhizosphere pH and redox potential, which regulate the root cell proliferation and mechanical properties (Bloom et al. 2003; Brix et al. 2002; Marschner and Römhild 1983). Because NH_4^+ dominates as the inorganic N source under anaerobic soil conditions due to the limitation of nitrification, NH_4^+ -tolerant wetland species ameliorate the toxic effect of excess NH_4^+ by exhibiting high GS activity for the quick assimilation of NH_4^+ compared with that of NH_4^+ -intolerant terrestrial plants (Balkos et al. 2010; Britto and Kronzucker 2002). As rice plants have isoenzymes of the cytosolic GS1 gene family (*OsGLN1;1* and *OsGLN1;2*) that can be classified into high-affinity subtypes with relatively high V_{max} , these GSs facilitate active NH_4^+ assimilation in their roots (Ishiyama et al. 2004). Studies on NH_4^+ metabolism in rice, maize, and tomato plants have reported that rice plants have much higher GS activity than the other species, and the GS activity increased more in the shoot tissues than that in the roots with the increase in NH_4^+ (Magalhaes and Huber 1991). This indicates that the GS activity is a key factor in the detoxification and assimilation of NH_4^+ in shoots of plant species with efficient NH_4^+ utilization (Magalhaes and Huber 1991). The ability to rapidly assimilate NH_4^+ not only in roots but also in shoots can also function as an N acquisition strategy in the wetland species growing under O_2 -deficient conditions. This is because the up-regulated N assimilation in shoots can lead to decrease in the demand for N assimilation in the roots, thereby decreasing root respiration and avoiding O_2 deficiency in roots (Fig. 5). When wetland wild grass and *Carex* species (*C. lyngbyei*, *C. lasiocarpa* var. *occultans*, and *C. middendorffii*) are grown in the sole NH_4^+ treatment under low O_2 condition, they exhibit a smaller root to shoot weight ratio (i.e., high S/R ratio) and increased net N uptake rate per unit root weight (NNUR) compared to the sole NO_3^- treatment. This high S/R ratio can lead to the decrease in the whole-root O_2 consumption

in the sole NH_4^+ treatment (Nakamura and Nakamura 2016; Nakamura et al. 2010, 2013) (Fig. 5). The decreased root growth (high S/R ratio) with sole NH_4^+ treatment is more prominent in species with weak O_2 -supply system with only diffusion than in species with strong O_2 -supply system with pressurized gas flow (Nakamura et al. 2013) (Fig. 5). Although the high NNUR causes high root respiration rate per unit root weight in species with low O_2 -supply system, the whole root respiration rate per shoot weight is similar between sole NH_4^+ and NO_3^- conditions due to the compensation for high O_2 uptake in roots by their high S/R ratio under sole NH_4^+ condition (Fig. 5). Thus, it seems that wetland plants primarily employ the NH_4^+ utilization strategy for N-acquisition, which enables them to acquire sufficient N for their growth and to minimize and regulate the whole-root O_2 consumption depending on the O_2 supply from shoots to roots (Fig. 5).

Even in anaerobic soil dominated by NH_4^+ , small amounts of NO_3^- are produced by oxidation in the soil due to the O_2 flux to the rhizosphere by species with active ROL (Brix et al. 2002; Kirk and Kronzucker 2005). When NH_4^+ -preferring species such as rice are grown under conditions where both NH_4^+ and NO_3^- are supplied, they show improved productivity and increase in the net N acquisition and ATP production (called “the synergistic effect of NH_4^+ and NO_3^- ”) compared with only sole NH_4^+ conditions (Kirk and Kronzucker 2005; Kronzucker et al. 1999; Li et al. 2006; Ying-Hua et al. 2006, 2007). Some studies have also reported the underlying mechanisms by which the addition of NO_3^- to an NH_4^+ containing soil increased the V_{max} value of NH_4^+ uptake and plasma membrane potential due to an increase in the number of NH_4^+ transporters, leading to enhanced growth and N uptake in rice plants (Ying-Hua et al. 2006, 2007). Moreover, the synergistic effect of NH_4^+ and NO_3^- in rice differs among varieties depending on the supply level of each inorganic N source and is genetically controlled (Ancheng et al. 1993; Ying-Hua et al. 2007). The synergistic effect of inorganic N has been studied in wild wetland plants. The synergistic effect of NH_4^+ and NO_3^- may be limited to species growing in habitats where nitrification occurs in their rhizosphere. Especially, the fast-growing species with high O_2 -supply system may display high ATP production and N acquisition under NH_4^+ -dominant soil conditions due to this synergistic effect (Fig. 5).

The acquisition abilities of each inorganic N source in the soil are different among species with different O_2 -supplying abilities even when they exist in similar habitats. *Phragmites australis* and *Zizania latifolia* are observed in the same habitat, but the abilities of O_2 supply are different. *P. australis* has a high ability of O_2 supply by the convective gas flow system and high ability of NO_3^- use owing to relatively high NR activity in roots under sole NO_3^- and low O_2 conditions. In contrast, *Z. latifolia* with only diffusion as the O_2 supply

breakdown and aerenchyma formation were induced when the cells were subjected to hypoxia (3% O₂). In contrast, no cell breakdown was reported in the overexpressing Hb line under the same growth conditions (Dordas et al. 2003). Most wetland plants can develop aerenchyma in their shoots and roots, but the mechanisms of aerenchyma formation and their development level may differ among species depending on their NO₃⁻ utilization ability and the NO levels. Further analyses are required to compare the effects of NO₃⁻ utilization on the aerenchyma formation among species with different O₂ supply capacities.

The formation of root cortical aerenchyma can also be induced by nutrient deficiency in the terrestrial species, maize (Hu et al. 2013). The formation of root cortical aerenchyma decreases the radial transport of nutrients by decreasing the living cortical tissue, which leads to a decrease in the maintenance requirements of living tissues of roots (Hu et al. 2013). Similarly, aerenchyma formation in wetland plants may contribute to not only avoid O₂ deficiency in root tips but also decrease the respiratory energy required to maintain the living tissues under O₂ limiting conditions. This saving of energy consumption by the aerenchyma formation may increase the allocation of the respiratory energy to other processes such as root growth and nutrient uptake. Some wetland plants with developed aerenchyma allocate their root respiratory ATP to maximize the N uptake instead of root maintenance and growth (Nakamura and Nakamura 2016). Such root responses in wetland plants could be their strategy for efficient O₂ consumption and high N acquisition for adapting to O₂ deficiency.

Conclusion

Wetland species with hypoxia and anoxia tolerance can regulate their carbohydrate level to maintain the glycolytic flux and reduce ATP consumption under O₂-deficient condition. At low O₂, NAD(P)⁺ regeneration by ethanol fermentation, sucrose degradation through the energy-saving SuSy pathway, and amino acid metabolisms such as glutamate, GABA, and alanine are common in both wetland and terrestrial species. Gene expression of α -amylase in the aleurone layer and storage organs at the germination and initial growth stages are limited to wetland species. Moreover, an effective tolerant function in the wetland species for surviving long-term hypoxic and anoxic conditions is caused by maintaining glycolysis through the reversible reaction catalyzed by PPDK and PFK-PP_i. In rice plant, cytosolic PPDK is more abundant in their roots than that in their shoots, and this may affect their adaptive response to frequent fluctuations in O₂ concentration. In post-hypoxic/anoxic stress, the metabolic change from glycolysis to gluconeogenesis and to the TCA

cycle contributes to normal metabolism during the recovery phase of re-oxygenation.

In wetland plants, the quick response of non-phosphorylating components, AOX and NDs, to the consumption of excessive reducing equivalents and avoidance of ROS and RNS production for maintaining mitochondrial homeostasis is effective in recovering from post-anoxic stress. However, the activation of these components would be futile in O₂ consumption and energetically burdensome under hypoxic condition. As some non-phosphorylating components are strongly co-expressed, precise coordination between the expressions and activities of these mitochondrial components can provide flexible ATP production and maintain cellular homeostasis in wetland species under more severe hypoxic and anoxic stresses.

The two strategies, LOES and LOQS, in wetland species reflect the different responses to O₂ deficiency and ATP production at subsequent post-hypoxic and anoxic stresses in their habitats. The difference in strategies could be due to the difference in the requirement of the reserved carbohydrates during the stress condition. Both LOES and LOQS in a single species are also reported. In wetland species with LOES, the developed aerenchyma and high O₂ supply system by the pressurized gas flow are effective in maintaining high O₂ availability to the roots, but not all plants have these functions. Further research on the interaction among hormones, O₂ availability, and primary metabolites is needed to understand their optimal balance among growth, escape, and quiescence to facilitate survival in their habitats. At low O₂ conditions, the efficient respiratory O₂ consumption in the roots of wetland species is carried out in soils with NH₄⁺ as the sole N source because these species can utilize NH₄⁺ without ARI. Some wetland species in which nitrification occurs due to their high O₂ supply system can also efficiently use the soil NO₃⁻. The differences in the preference for N sources among wetland species could also be ascribed to the differences in their anaerobic ATP production systems. The species with high ability of NO₃⁻ utilization can use the NO₂⁻-driven ATP production system, and the species specialized for NH₄⁺ utilization can use the fermentation system. The different N utilization strategies for ATP production may be functionally linked to hypoxia tolerance in wetland species. Thus, further exploration of the ecophysiological mechanisms of aerobic and anaerobic respiratory responses to the N sources in roots of wild wetland species is needed to completely understand the anaerobic stress before global climate change makes the stress more severe.

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