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REVIEW ARTICLE

Physiological and biochemical changes in plants under waterlogging

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Abstract Waterlogging usually results from overuse and/or poor management of irrigation water and is a serious constraint with damaging effects. The rapidly depleting oxygen from submerged root zone is sensed and plant adjusts expressing anaerobic proteins. Plant cells shift their metabolism towards low energy yielding anaerobic fermentation pathways in the absence of oxygen. Structural modifications are also induced as aerenchyma formation and adventitious rootings, etc. Studies at molecular and biochemical levels to facilitate early perception and subsequent responses have also been worked out to produce resistant transgenic plants. This review explores the sequential changes of plant responses at different levels regarding their defense strategies and efforts made to enhance them, tailoring crucial regulators so that they can withstand waterlogging stress.

Keywords Waterlogging · Hypoxia · Physiology · Biochemistry

Abbreviations

O_2^-	Superoxide
RNS	Reactive nitrogen species
ANPs	Anaerobically induced polypeptides
ACC	1-Aminoacyl cyclopropane-1-carboxylic acid
C_i	Internal carbon dioxide
CER	CO_2 exchange rate
SuSy	Sucrose synthase
CAT	Catalase
POX	Peroxidase
SOD	Superoxide dismutase
PM-NR	Plasma membrane–nitrate reductase
cNR	Cytosolic nitrate reductase
ADH	Alcohol dehydrogenase
Hb	Hemoglobin
xet-1	Xyloglucan endotransglycosylase-1
PGA	3-Phosphoglycerate

Introduction

The soil water content of surface layer whenever exceeds at least 20% higher than field's carrying capacity it leads to free standing water on soil surface (Aggarwal et al. 2006; Nilsen and Orcutt 1996). This condition imposes severe constraints on crop growth and productivity (Jackson and Colmer 2005). Waterlogging stress may develop due to several direct (improper irrigation practices) and indirect (global warming) anthropogenic and natural consequences (meteorological) leading to altered plant metabolism, architecture and eco-geographical distribution depending upon plant responses. Alarmingly changing earths' average temperature (IPPC 2001) is predicted to exaggerate the problem in near future. The erratic rainfall, rise in sea level due to increasingly melting glaciers and shift in native climate-spectrum will pose selection pressure on agricultural crops. Therefore, highly resistant plants mingled with desired agronomical traits will be the demand of future crops. Rice, the global staple crop feeding above the half of the globe, has secured its growth in different climatic regimes accompanied by

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genotype selection. The other economic cereals (as *Triticum, Pennisitum* and *Zea mays*, etc.) however, do not appear to this fortunate overriding the detriment of waterlogging for their survival. Also rice, however, cultivated on flooded anaerobic soils (Swaminathan 1993), when submerged completely; seedlings suffer oxygen deficiency as is the case in Southeast Asia (Jackson and Ram 2003).

Flooding generates hypoxic stress in plants

Land plants are strictly aerobes receiving freely diffusing molecular oxygen from aerial even underground tissues. Oxygen deficiency (hypoxia) or its complete absence (anoxia) damages most often the roots and seeds under transient or sustained flooded soil in various countries (Maltby 1991). Excess water produces anoxic soil within a few hours (Gambrell and Patrick 1978). The slow diffusion rate (10^{-4} fold), low solubility (Ponnamperuma 1984; Gambrell et al. 1991) and increased microbial activity not only reduces the soil oxygen content, but also latter adds the toxic organic and inorganic compounds in the soil (Ponnamperuma 1984; Gambrell et al. 1991). The condition deteriorates during high temperature and in night, when root respiration increases with simultaneous increase of microbial activities. This rapidly depletes oxygen from soil rendering it with reduced inorganic forms of Fe^{3+}, S^{2-} and carboxylic acids, etc. Redox sensing of O_2 induces various biochemical, and therefore physiological changes in roots and shoots of several dicots, such as, in *Lycopersicon esculentum* (Jackson and Campbell 1976; Bradford and Yang 1981; Bradford and Hsiao 1982), *Solanum tuberosum*, legumes, *Nicotiana tobaccum*, *Ipomoea batatas*, *Cucumis sativus*, and monocots as in *Oryza sativa* (Vartapetian et al. 2003; Perata et al. 1992), *Triticum aestivum*, *Z. mays* (Saglio et al. 1988), and *Arabidopsis thaliana* (Trevaskis et al. 1997; Wang et al. 2000). A short spell of flood, however, may spare some moderately tolerant crops with the induction/up-regulation of counteracting genes to reverse the damages accompanied, at the cost of de-repression of certain other genes required for growth acceleration. A slow diffusion rate of O_2 under water pushes the plant (especially roots) towards more anaerobic biochemical acclimation (Armstrong 1978). Thus plants shift their metabolism at basal metabolic rate (BMR) to sustain their survival under low energy economy. Moreover, stagnate flooded water in lowland with added high precipitation climates may lead to sustained partial or complete waterlogging (submergence) may lethally push plant metabolism beyond BMR, where it my die ultimately. Therefore, the duration of waterlogging and genotype has critical relevance in stress defense. The mass destruction of crops causes a large reduction of global productivity every year. Reduced supply of adenylate pool set back the plant metabolism to anaerobiosis, by finely modulating the tissue based biochemical set up. However, rice employs this strategy at its initial level of seed germination avoiding hypoxia by extensing coleoptile to reconcile with air (Jackson and Pearse 1991) and transporting oxygen from aerial part to hypoxic/anoxic roots indicating spatial and temporal pattern of the two strategies (true tolerance and avoidance, respectively) balancing under different growth and climatic conditions. Upsurge in massive literature in recent past regarding the defense strategies elicited by rice under flooding and related phenomena is indicative that rice has been at the center of researches. Since waterlogging is soon followed by hypoxia, rice switches towards anaerobic metabolism particularly in roots. This condition hastens the aerobic mode of energy production with decline in adenylate pool.

Waterlogging upregulates ACC in root tips as primary signal

Under abiotic stress conditions the reduced plant growth is noticed first. Since roots are the anchoring and absorptive system of plants associated with mineral and water absorption, microbial interactions and various other signaling events, these are crucial for sensing several environmental (edaphic) cues. The transition to hypoxia generates the reactive oxygen species (ROS) in roots with the concomitant production of H_2O_2, a well known signaling molecule. Plant life had evolved 460 million years ago in excess water conditions (Beerling 2007). Roots possess the most important tissues ascertaining the aerial life of plants on land. Roots of aerial plants are composed of tightly packed tissues with very little intercellular spaces allowing slow diffusion of gases (Geigenberger 2003). On the other hand, aquatic or semi-aquatic/amphibious plants have several air chambers in their root anatomical structures. Waterlogging in mesophytes, severely slow down (10^{-4} fold) the rate of oxygen diffusion in root tissues. Unavailability of oxygen induces ANPs including the induction of ACC, a precursor of ethylene biosynthesis. ACC is well known to be produced under anaerobic and/or anoxic conditions. This signal is transported to aerial parts of shoot. ACC in the presence of O_2 and ACC-oxidase forms ethylene. The conversion of ACC to ethylene could be assumed as a major determining factor in achieving resistance, facilitating various regulatory functions in plants. Induction of apoptosis in selected tissues/cells (Subbaiah and Sachs 2003), nodal adventitious rooting, formation of air chambers, and metabolic changes under anaerobiosis and several other functions were attributed to be regulated by the ethylene, which is synthesized from its precursor ACC transported from roots. Initial PCD events sometimes are considered to be survival strategies.

Waterlogging stimulates root tip death

Meristems are the first target of stresses as dispensable tissues. Besides the ceased growth of shoot apical meristems, root tips are more sensitive to water borne hypoxia in soil particularly in mesophytes. Maize root tips were shown to progressively accelerate towards PCD as waterlogging/anoxia persists. A considerable attention has been paid to strategies/mechanisms that prolong the anoxia tolerance to the primary root tip in young maize seedlings (Drew et al. 1994). The maize root tips that are not hypoxically acclimated are very sensitive to anoxia and die within few hours (Roberts et al. 1984; Johnson et al. 1989). While in some maize genotypes accelerated PCD appears to be genetically controlled tolerance mechanism (Zeng et al. 1999). Induced mRNA expression of xyloglucan endotransglycosylase-1 (*xet*-1), a putative cell-wall-loosening enzyme (Peschke and Sachs 1994; Saab and Sachs 1995, 1996) in maize root tip indicate its involvement in root tip death. The induction of *xet*-1 appears to be specific to O_2 deprivation (Peschke and Sachs 1994).

Flooding and induction of aerenchyma formation

As this signal (ACC) progresses towards more aerobic shoots, its conversion to ethylene by ACC oxidase (Voesenek et al. 1993) induces auxin-mediated aerenchyma formation in the region just below the root tip (Drew et al. 1981) in number of crop species viz. rice (Justin and Armstrong 1991), wheat (Watkin et al. 1998), maize (Gunaverdena et al. 2001), barley (Arikado and Adachi 1955), and soybean (Bucanamwo and Purcell 1999), etc. These cortical air spaces facilitate aeration and assure prolonged survival (Drew et al. 2000). The enzymes like cellulases (Drew 1992; Grineva and Bragina 1993; He et al. 1994) alongwith other degrading enzymes (Campbell and Drew 1983; He et al. 1994) viz. xyloglucan endotransglycosylase-1 (*xet*-1) (Peschke and Sachs 1994; Saab and Sachs 1995, 1996), expansins (Voesenek et al. 2003; Vriezen et al. 2003), and pectinases are likely to be involved in lysigenic aerenchyma formation. Investigations are also going on the illusive role of NO concerning with PCD and aerenchyma formation.

The epidermal and exodermal barriers formed in roots facilitate oxygen (Aschi-Smiti et al. 2004; Colmer 2003) and ethylene entrapment. The lysigenous aerenchyma formation by ethylene is mediated by expressing several apoptosis related ANPs, *xet-1*, proteases, death inducing factors (Subbaiah and Sachs 2003). Growth is redirected as vertical extension of shoot at the cost of sacrificed compact tissues in certain cases, which are more habituated to submergence (as *Potamogeton pectinatin*, wheat, rice, etc.) to shorten the total submergence and reuniting the shoots with air (Voesenek et al. 2003) even in complete absence of oxygen and independently of ethylene (Visser et al. 2003). This strategy appears to be providing resistance to withstand flash-flood to those previously experienced mild dose of waterlogging or those partially adapted to flood. Such changes may also be supported by the auxin favored expression of expansins (Voesenek et al. 2003; Vriezen et al. 2003), *xet-1* and pectinases when pH is lowered due to accumulation of lactate, organic acids etc. under anaerobiosis.

Waterlogging-mediated epidermal cell-death facilitates emergence of adventitious roots at nodes

Programmed cell death (PCD) is a part of development, has been studied by a number of researchers at different stages of growth viz. gametophyte (Buckner et al. 1998), embryo development (Marubashi et al. 1999) and germination (Wang et al. 1996a, b; Fath et al. 1999), xylogenesis (Groover and Jones 1999), root-cap formation, senescence, plant defense strategies (Dangl et al. 1996), and in adaptation to low oxygen stress when cortical cells are sacrificed to form aerenchyma (He et al. 1996; Kawai et al. 1998; Samarajeewa et al. 1999). In nodal tissue also, adventitious root initials remain covered by the epidermis until the proper signal induces them to accelerate their growth rate and to emerge. They are formed early in the development (Lorbiecke and Sauter 1999). During flood when ethylene accumulates at nodes, it causes death of epidermal cell covering the tip of primordia facilitating emergence of root (Mergemann and Sauter 2000) at water surface and providing aerenchyma ample of oxygen in deep water (rice). The interaction of auxins and ethylene is important for the induction of adventitious root formation (McNamara and Mitchell 1989, 1991).

Submergence affects leaf-gas exchange

Submergence when inundates shoots as well as roots sufficiently, it prevents the aerial influx of CO_2 and light decreasing the photosynthesis largely. However, a sustained partial submergence could also affect leaf gas exchange in photosynthetic aerial parts.It has been reported that flooding cause stomatal closure directly, without influencing the photosynthetic capacity, in *Vaccinium ashei* (Davies and Flore 1986a, b), therefore decreasing C_i (Liao and Lin 2001). The systemic signal for this is assumed to be translocated from roots to leaves. Ethylene regulates the expression (and activity) of ABA in mesophylls. The increase in foliar ABA content in peas when subjected to soil flooding was accompanied by closure of stomata (Jackson and Hall 1987). Similar results have been observed in tomato (Jackson 1991). In most of the flood-intolerant plants, flood cause a significant decrease in foliar gas exchange capacity, for instance, wheat (Trought and Drew 1982), tomato (Bradford 1983), *Pisum sativum* (Jackson and Kowalewska 1983), *Citrus* sp. (Phung and Knipling 1976), etc. However, some flood-tolerant plants have developed adaptive mechanisms so as to maintain better photosynthetic capacity (Sena Gomes and Kozlowski 1980; Topa and Cheesemann 1992). Leaf gas exchange is directly related to the photosynthetic capacity of plants. As flood inundates plant internal CO_2 concentration (C_i) increases linearly despite of reduction of stomatal conductance. A decrease of stomatal conductance was found to be correlated with an increase of leaf water potential in flooded bitter melon (Liao and Lin 1994). It can be hypothesized that stomatal closure slows the rate of transpiration, thus preventing leaf dehydration (Bradford and Hsiao 1982). In control and flooded plant, stomatal conductance was shown to be correlated with CO_2 exchange rate (CER) (Smith and Ager 1988; Vu and Yelenosky 1991; Liao and Lin 1994). These results imply that stomatal aperture is a limiting factor for CER. Despite the reduced CER, foliar C_i was reported sufficiently high as compared with plants that had not been subjected to flooding. The observations suggest that stomatal aperture is not the only limiting factor for CER but is partly responsible for the decrease in the photosynthetic capacity of mesophyll tissue. Also rate of respiration sufficiently increases during flooding stress. Following factors could be suggested for elevated C_i, (1) reduced photosynthetic capacity (2) increased respiration rate, and (3) decreased stomatal conductance.

Physiological changes under flooding

Submergence reduces activity of Rubisco and photosynthetic capacity of mesophyll cells

The activation level of Rubisco in flooded bitter melon increased above the control value after 1 day of flooding and subsequently declined to a lower level (Liao and Lin 1994). Change in the level of activation of Rubisco reflects the level of carbamylation of Rubisco (Miziorko and Lorimer 1983), which in turn is regulated by C_i and light intensity (Sage et al. 1990). In general, the activation level of Rubisco generally declines as C_i increases (von Caemmerer and Edmondson 1986; Sage et al. 1988, 1990). The activity of Rubisco increases initially with increase in C_i then declines as C_i further increases (Liao and Lin 1994). Under elevated C_i, the pool size of RuBP was found to decline and the level of PGA to increase in three different plant systems (Badger et al. 1984; von Caemmerer and Edmondson 1986; Sage et al. 1988). (Sage 1990) suggested that excessive consumption of RuBP may switch off the active site of Rubisco, thus maintaining a balance between RuBP consumption and its regeneration, and regulating the activation of Rubisco. It has been established that the carbamylation/decarbamylation equilibrium of Rubisco involves reversible active enzyme-CO_2-Mg^{2+} complex formation. Formation of this complex is pH dependent and has been observed in leaf homogenates (Lorimer et al. 1976) and isolated chloroplasts (Bahr and Jensen 1978). At a concentration of 0.2 M Mg^{2+}, optimal Rubisco activity was found to be between pH 8.5 to 10, whereas 90% of the enzyme activity was lost when the pH was lowered to 7.0 (Lorimer et al. 1976). Andrews and Lorimer (1987) postulated that a high level of CO_2 favors overproduction of PGA and leads to acidification of the stromal phase, thus reducing the carbamylation level of Rubisco. Since Rubisco catalyzes the initial reaction during the assimilation of atmospheric CO_2 (Andrews and Lorimer 1987), the activation level of Rubisco should be positively correlated with the rate of photosynthesis. Reduced quantity of Rubisco protein as well as reduced activity of existing enzymes may cause Rubisco activity to decline during flooding. Furthermore, it was reported that phloem transport of photosynthates was blocked (Saglio 1985), and that the demand for sucrose loading was lowered. This may lead to an accumulation of starch in the chloroplasts (Wample and Davis 1983; Liao and Lin 1994). It can, thus, be suggested that feedback inhibition of starch accumulation may result in a reduction of CER in flooded plants. The many physiological responses observed indicate that both stomatal and metabolic factors are responsible for the reduction of CER during flooding stress.

Waterlogging cause reduction in leaf-water-potential

Inhibition of aerobic respiration with concomitant loss of ATP synthesis in roots ceases the ion uptake and transport (Huang et al. 2003; Vartapetian et al. 2003) through fueled channels. This disturbs the water potential across the cells in root tissues, thus lead to breakdown of homeostasis. Localization of ABA causes various effects viz. increased ion flux (K^+ outflow), stomatal closure (Davies and Zhang 1991), and cell growth inhibition. ABA-mediated increased hydraulic conductivity across the membrane appears to be due to its altered properties (Van Steveninck and Van Steveninck 1983). Loss of ATP perhaps fails to maintain membrane potential and loss of ions alongwith ABA-mediated K^+ outflow causes collapse of guard cells. The turgor loss ultimately results in plant wilting within hours to days of flood (Jackson and Drew 1984).The ethylene and

ABA-mediated curvature of leaves occurs due to reduced abaxial growth of petiole. A differential cell growth causes epinasty in leaves and loss of turgor, the leaf wilting. Since ABA is well known as a Ca^{2+} antagonist, the inhibition of (IAA and cytokinin mediated) growth may be due to interference with Ca^{2+} metabolism.

Waterlogging mediated reduced translocation checks the localization of photosynthates

Accumulation of starch has been reported in leaves of various flooded plants, e.g., *Helianthus annuus* (Wample and Davis 1983), *Citrus sinensis* grafted onto rough lemon and sour orange rootstocks (Vu and Yelenosky 1991), *Pinus serotina* (Topa and Cheesemann 1992), *M. charantia* (Liao and Lin 1994), *L. cylindrical* (Su and Lin 1998) and *S. samarangense* (Hsu et al. 1999; Wample and Davis 1983). It could be assumed theoretically that if the translocation path was blocked, assimilates in leaves would not be able to reach the roots, resulting in a sugar deficiency in the roots. However, the sugar level in flooded roots of certain plants was found to be higher than that in the unflooded control, as in bitter melon (Su and Lin 1998). The successful germination of seeds under anoxia is found to be dependent on successful induction of α-amylase, the enzyme responsible for the degradation of reserved starch in seed endosperms (Perata et al. 1992). Studies showing decline in starch level and initial rise in soluble sugars (Barta 1988 and Castonguay et al. 1993; Su and Lin 1998) as sucrose and hexoses (glucose and fructose) during early flooding period followed by a fall culminating to like those of controls. It indicates that starch reserves in roots are mobilized and can readily provide sugars for anaerobic metabolism in flooded roots (Perata et al. 1992). A long term flooding, however, leads to eventual necrosis of flood intolerant cultivars and death ultimately (Liao and Lin 1995; Su and Lin 1998). Continuous supply of fermentable sugars to roots is considered to be critical for long term survival of peas, pumpkin, and several herbaceous plants under anoxia/flooding (Jackson and Drew 1984; Saglio et al. 1980; Webb and Armstrong 1983).

The total nitrogen content in plant tissue has been reported to decrease under flooding stress in various fruit species, such as citrus (Labanauskas et al. 1972), apple (Olien 1989), avocado (Slowick et al. 1979), and blueberry (Herath and Eaton 1968). In the wax-apple tree, the total nitrogen in the leaves was found to be significantly lower after 35 days of flooding treatment compared with the unflooded control while the total amount of carbohydrates increased, resulting in a significant increase in C/N ratio (total carbohydrate/total nitrogen) (Hsu et al. 1999). The carbohydrate–nitrogen ratio in fruit trees has often been related to bud formation, flowering, and fruiting, but this relationship also varies with the species (Goldschinidt 1982; Scholefield et al. 1985; Smith et al. 1986).

It has been reported that SuSy has a critical role in sucrose hydrolysis in anoxic tolerance of maize roots (Recard et al. 1998) using double mutant *sh1 sus1*. (Zeng et al. 1999) reported in hypoxic maize seedlings that of the two enzymes involved in sucrose hydrolysis, the activity of invertase is down regulated while that of sucrose synthase is upregulated. (Aschi-smiti et al. 2004) reported that 30-day-old plants of *T. subterranium* 15 days of hypoxia showed induction of sucrose synthase, fructose kinase lactate dehydrogenase enhanced-ethanol production and improved energy charge in association with hemoglobin induction. Content of reducing sugar increases under waterlogging and was parallel to SuSy activity (Sairam et al. 2008). Since roots and rhizome are essentially aerobic organs, the consequences can be fatal, as aerobic respiration ceases, level of energy rich adenylates drop rapidly, causing a drastic decline in ion uptake and transport (Huang et al. 2003; Vartapetian et al. 2003).

Phytohormones regulate plant modifications under flooding stress

Phytohormones are integrating metabolites instead of controlling agents therefore, often regarded as growth regulators (Jain et al. 2006). Thus response elicited by them is not amount based rather based on sensitivity of tissue (Moore et al. 1995). ACC is primary root signal transported from roots to aerial parts under very early stages of hypoxia (Bradford and Yang 1980), therefore, appears to have critical role providing resistance in rice cultivars. ACC oxidase requires the exposure of molecular oxygen for the biosynthesis of ethylene (Bleecker and Kende 2000). Ethylene production is slowed by partial oxygen shortage (Raskin and Kende 1984) favoring the accumulation of ACC. ACC is supposed to antagonize the polar transmission of auxins hampering the elongation of shoot. Flooding induced compromised lengthening (Jackson 2008; Braendle and Crawford 1999) could be attributed to inability to conversion of ACC to ethylene due to absence of O_2. However, when it is converted to ethylene (may be due to conservative use of oxygen stored in air chambers or bind with Hb), it is known to interplay with auxins facilitating escape elongation of rice to access oxygen. The tissue compactness may be loosened to facilitate extended growth accompanying selected tissue sacrifice, e.g., lysigenous aerenchyma formation. Ishizawa and Esashi (1984) suggested interaction of ethylene and IAA as increased level of IAA has been found in elongating rice coleoptile (Pegoraro et al. 1988). A lower ABA synthesis under anoxia (Hoffmann-Benning and Kende 1992) may aid extension to avoid its negative effects (Mapelli et al. 1995). Ethylene plays a vital role under hypoxia in escape elongation of rice to access oxygen, CO_2, and light (Jackson and Pearse 1991; Jackson 2008). However in sensitive varieties or other species, polar transmission of auxins when checked (may be due to the antagonistic effect of ACC), result in hampered shoot growth. This could be correlated with ceased hydraulic conductivity or water transport through shoot. Ethylene accumulates in submerged plant parts higher than normal concentrations (Musagrave et al. 1972) due to ten times slower release into water (rather soil air) from root (Stunzi and Kende 1989) and increased synthesis (Jackson 1985). The interaction of auxin and ethylene is important for the induction of adventitious root formation (McNamara and Mitchell 1989) too. Soluble sugars are rapidly channeled to fermentative metabolism when the oxygen level falls. This limited amount of soluble sugars is utilized conservatively under finely tuned interactive regulation of phytohormones with sugar signals (Loreti et al. 2003). Swelling of base and growth retardation is well known functions mediated by ethylene under hypoxia.

NO at low concentration has been found to be involved in regulation of diverse biochemical and physiological processes in plants viz. seed germination, hypocotyl growth, defense responses, stomatal closure, and apoptosis (Giba et al. 1998; Beligni and Lamattina 2000; Koprya and Gwozdz 2003; Delledonne et al. 1998; Durner et al. 1998; Kim et al. 1998; Neill et al. 2003). NO might be playing a crucial role in signal transduction and PCD during aerenchyma formation. Ethylene enhances water transport in hypoxic Aspen (Kamaluddin and Zwiazek. 2002). Ethylene induces activity of hydrolytic enzymes in adventitious maize roots, under the conditions of advancing flooding (Peschke and Sachs 1994; Saab and Sachs 1996). Stomatal resistance is further associated with induction of ABA synthesis and its localization. ABA and ethylene both are regarded accelerating senescence independently (Zacarias and Reid 1990). ABA appears to initiate while ethylene appears to exert its effects at a later stage (Gepstein and Thimann 1981).

Biochemical changes under flooding stress

Production of ethanol and lactic acid though well-known fermentation pathways, is one mechanism that organisms use to provide glycolytic substrate oxidation and ATP synthesis, maintaining short term cell viability under hypoxic conditions. The substrates to feed these pathways are also increased by increasing the flux of glycolysis. ATP synthesis required to maintain plant growth and viability in an aerobic environment is achieved by the oxidation of carbon sources using oxygen as an electron acceptor. Under conditions that limit oxygen availability complete substrate oxidation is restricted by the lack of an electron acceptor. Two pathways are put forth yet so far operating under hypoxia, (1) anaerobic fermentation pathways and (2) alternative pathways, e.g., Hb–NO cycle (Sairam et al. 2009).

Anaerobic fermentation pathways under waterlogging generate hypoxia

Protein profile is changed under anoxia and specific proteins are synthesized called ANPs (anaerobic polypeptides) (Sachs and Ho 1986). Most of the ANPs are glycolytic enzymes (Miernyk 1990; Mujer et al. 1993). Anoxic condition replaces mitochondrial oxidative phosphorylation with that of anaerobic fermentation to meet the cellular energy demand (Davies 1980). The predominance of ADH (Sachs et al. 1980) and its isozymes (Harberd and Edwards 1983; Liao and Lin 1995) are also reported. ADH is the key regulator to let glycolysis run by supplementing depleting demand of NAD^+ (Saglio et al. 1980). The ADH induction with concomitant production of ethanol is well studied by McManmon and Crawford 1971; Avdhani et al. 1978; Chirkova 1978; Smith and Rees 1979; Tripepi and Mitchell 1984. Crawford (1967) proposed the "metabolic theory" indicating that plant achieves anoxia tolerance by minimizing the ethanol production re-routing the ethanol fermentation to malate synthesis (Crawford 1967; McManmon and Crawford 1971). Alternatively, (Vanlerberghe et al. 1990), preferred succinate over malate, as an end product of fermentation wherein partial TCA form fumarate via oxalo-acetate and malate regenerates NAD^+. Davies (1980) proposed "pH-stat hypothesis" wherein he explained that short term tolerance of flood favours ethanol instead of lactate, as later elevates cytoplasmic acidosis (Roberts et al. 1984). Latter on this notion was further supported by (Vartapetian et al. 2003) and it was concluded that actually, plant cell increases the ethanol production to achieve hypoxic tolerance under prevailing conditions of waterlogging (Vartapetian 2005, 2006). The switch that occurs from the aerobic TCA cycle to fermentation pathways forming lactate and ethanol under hypoxic and anoxic conditions is accompanied by a decline in pH due to ATP hydrolysis and lactate accumulation (may not occur in some hypoxic tissues) (Saint-Ges et al. 1991; Kennedy and Rumpho 1992; Ratcliffe 1995; Gout et al. 2001; Ooume et al. 2009). Furthermore, lower activity of pyruvate decarboxylase (PDC) suggest it to be rate limiting for ethanol production rather ADH itself in flooded roots. Accumulation of ethanol, however, has not been reported to be directly involved in the growth suppression, though decrease ATP and increased pH of apoplastic solution may directly be involved in growth suppression (Ooume et al. 2009). The decline in pH slows the rate of lactate formation and activates PDC diverting glycolytic carbon flow to ethanol formation. Activity of lactate dehydrogenase (LDH) increases 20-fold during prolonged hypoxia, which may be an important factor contributing to long-term adaptation to hypoxia (Hoffman et al. 1986). Investigations also revealed the induction of transcriptional activation of glycolytic and ethanol fermentation enzymes viz. PDC (Kelley 1989; Peschke and Sachs 1993), ADH (Gerlach et al. 1982; Rowland and Strommer. 1986; Andrews et al. 1994), glucose peroxidase isomerase (Kelley and Freeling 1984a), aldolase (Kelley and Freeling 1984b), and glucose peroxidase dehydrogenase (Martinez et al. 1989; Russel and Sachs 1989).

Under waterlogging osmotic concentration of the cell sap substantially decreases via decreased concentration of organic compounds as sugars, amino acids etc. (Ooume et al. 2009). Increased secondary metabolism is also reported under waterlogging stress with the upregulation of concerned enzymes viz. phenylalanine ammonia lyase (PAL), tyrosine ammonia lyase (Alla et al. 2002; Ahsan et al. 2007), flavanone 3-hydroxylase (Ahsan et al. 2007). The increased production of phenols (benzoic, 2-hydroxybenzoic and 4-hydroxybenzoic acids) and monocarboxylic acids (formic, acetic, and propionic acids) caused a substantial shift towards steady K^+ efflux, accompanied by an immediate net influx of H^+ is reported in sensitive varieties (Pang et al. 2007).

Waterlogging and role of Hb/NO cycle

Nitrate reductase plays a very crucial role reducing nitrate to nitrite. Enzymes linked to nitrate reduction pathway synthesized de novo (Mattana et al. 1994) and suggested the link with concomitant prevention of acidification during hypoxia (Steffen et al. 2001). Among two types of NR reported (cNR and PM-NR), two third of root nitrate reduction can be attributed to PM-NR (Gojon et al. 1986). NR activity is tightly regulated by the phosphorylation/de-phosphorylation, substrate and co-factor feed back and enzyme degradation. The phosphorylated form is inactivated with 14-3-3 protein and activated again by cNR phosphorylase. Hypoxial activation of NR is about 2.5 fold greater at acidic external pH (4.8) (Botrel and Kaiser 1997).

Huffaker's group initially demonstrated PM-NR activity and is present only in root tissue with optimum activity during night (Stohr and Mack 2001). Since succinate is a preferred electron donor over NAD(P)H and it hyper-accumulates during hypoxia (Fan et al. 2003), it possibly can play role in nitrate reduction at plasma membrane. Fumarate may reduce back to succinate by succinate dehydrogenase using complex I and reduced ubiquinone (Cecchini 2003) under hypoxia.

When nitrate supplied exogenously as $N^{15}O_3^-$, radioactive N^{15} appears in amino acids in rice (Reggiani et al. 1993; Fan et al. 1997). Alanine formation is strictly induced during hypoxia (Magneschi and Perata 2009). Furthermore, 70% excess NADH under alanine synthesis might have been recycled via NO_3^- reduction to ammonium (Gibbs and Greenway 2003). NH_4^+ ion produced can be incorporated into glutamate via glutamine synthetase-glutamate synthase (GS-GOGAT) enzyme system using NADPH and ATP or via reverse glutamate dehydrogenase using NAD(P)H (Gibbs and Greenway 2003). A part of glutamate may facilitate pH regulation by conversion into gamma amino butyric acid. A partial TCA cycle may maintain 2-oxoglutarate (Igamberdiev and Gardestrom 2003). However, it should be noted that nitrite reductase; a key branch to alanine production is inhibited under hypoxia (Botrel et al. 1996), also alanine does not accumulate in sufficient amount. (Fan et al. 1997) reported a lower rate of ethanol production in rice coleoptiles supplied with NO_{3-} in comparison with those supplied with NH_4^+. This data indicates, a plausible diversion from nitrite reduction, strengthening NO to be considered as a possible product.

Nitrite-NO reductase bound to plasma membrane could be considered as a putative candidate for the reduction of NO_2 to NO, formed by PM-NR (Stohr et al. 2001). However, physiological electron donor could here be either Hb or cytochrome other than cytochrome c (NO is a potent inhibitor of cyt-c oxidase) (Zottini et al. 2002). A heme protein oxidized during the reaction can be reduced by a protein with cyt-reductase activity. (Hill 1998) reported the existence of nonsymbiotic (class II) Hb induced under low ATP level of cell (Nie and Hill 1997) or increasing sucrose in *Arabidopsis* (Trevaskis et al. 1997). It maintains the cell energy state under hypoxia in maize cell lines (Sowa et al. 1998). The hypoxia induced increase of Hb level in *Arabidopsis* under elevated nitrate supply modulates NO level (Wang et al. 2000) and also regulates the generation of NAD^+ (Hill 1998). (Sowa et al. 1998) observed reduced CO_2 production and ADH activity in transformed maize cell lines. Hypoxic conditions also provide optimum pH (6.1) for Ni-NOR for its activity. It has been shown that it can utilize even 100 μM concentration of nitrite, showing its higher $V_{\max}$ (Stohr et al. 2001). Class I Hb may also have possible role in maintaining lower NAD(P)H/NADP ratio under anaerobiosis (Igamberdiev et al. 2004b). An oxy-hemoglobin would donate negatively charged di-oxygen to NO forming NO_3^-

and met-hemoglobin (Di Iorio 1981). In nodule of leguminous plants met-hemoglobin reductase has been demonstrated (Topunov et al. 1980) to reduce met-hemoglobin to hemoglobin. Besides these, Cyt-b5 reductase of endoplasmic reticulum (Hagler et al. 1979) and dihydrolipoxide dehydrogenase (Moran et al. 2002; Igamberdiev et al. 2004a) were also reported to possess met-hemoglobin reductase activity.

Hypoxia induces nitrate respiration

Evidence has been accumulating of a putative "nitrate respiratory pathway" capable of generating a proton motive force in bacteria (Jormakka et al. 2003). The presence of such a pathway in plants potentially generating ATP under anoxia more efficiently might explain less carbon flow under nitrate supplement than under ammonium (Fan et al. 1997). However, no ATP synthase has been identified in eukaryotic plasma membranes and those which are present (P-type ATPases), are unable to synthesize ATP. Recently, Igamberdiev and Hill (2009) put forth evidence that nitrite can substitute from oxygen at the terminal cytochrome oxidase step thereby allowing it electron transport to proceed, to a degree, anaerobically.

Perhaps nitrate is the second abundant molecule economically available that cell can use to substitute O_2 to receive electron in electron-transport-pathway; when O_2 is depleted. Under anaerobiosis, number of mitochondria decreases in cell. Cytoplasmic acidosis could not be tolerated for long time as most of the anaerobic enzymes are cytosolic. The H^+ is sequestered either to vacuole or out of plasma membrane. There must be activation of specific type ATPases functioning as ATP synthases to break this gradient to couple with ATP synthesis. Since P-type ATPases of plasma membrane are precluded for their role as ATP synthesis, tonoplast might be speculated to perform this responsibility in plants.

Role of antioxidant system under waterlogging stress

Reactive oxygen species are produced at the transition when plant or its any part either enters to hypoxia/anoxia from normoxic conditions or it return to aerobic environment. In natural course ROS including O_2^-, H_2O_2, OH^- (Asada 1999; Dat et al. 2000), and NO (Wink and Mitchell 1998; Lamattina et al. 2003) are produced or leaked excessively under stress. In germinating seedlings also, ROS production was reported (Bailly 2004; Bouteau and Bailly 2008). After waterlogging, sub-terrestrial organs like roots and rhizomes are more prone to oxidative shock under such conditions.

These ROS if generated in larger quantity may oxidize proteins, lipids and nucleic acid and leading to even mutation (Halliwell and Gutteridge 1999). However to neutralize the toxicity of ROS plants have evolved an endogenous system of enzymes (e.g., catalase, peroxidase, SOD, etc.) and metabolites (e.g., ascorbate, glutathione, Tocopherol, and proline) to operate it, if exposed to stress (Apel and Hirt 2004). A fine tuning between ROS and scavenging molecules monitors the growth and cellular expression under normal conditions. However, their production is more often obvious during resetting the biochemical set up during stress, where plant compromises growth to redirect these molecules for new functions. Therefore, in the interim between return to aerobiosis and reactivation of electron transport chain favors the ROS production. Imbalance between scavenging and production of ROS due to alteration in biochemical set-up under stress may leak excess ROS. Altered membrane properties in leaves fails to sustain turgidity may cause osmotic stress favored by reduced water transport, which in turn presumably decrease SOD and CAT activity and overproducing O_2^- as reported in wheat leaves. This in turn causes exacerbation of lipid peroxidation and depression of photosynthesis. The steady state level of ROS in different cellular compartments is determined by interplay between multiple ROS producing pathways and ROS scavenging mechanisms. They are controlled by the ROS signal transduction pathway and believed to run a "ROS-cycle".

Recent findings of new roles of such species (ROS and free radicals) are attributed to control and regulate various biological processes viz. PCD, hormonal signaling, stress responses, and development. The burst of ROS is reported during various defense mechanisms in biotic stresses (causing localized necrosis and/or PCD) or in intense abiotic stresses. In cell(s)/tissue (s), there appears an adjustment (when stress accelerates) between PCD and necrosis till the death; dispensable tissues/organs are sacrificed first. New centers of origin of ROS production recently identified include NADPH oxidases, amine oxidases, and cell-wall-bound peroxidases etc. NO acts as an inter/intra-cellular signaling plant growth regulator (Beligni and Lamattina 2000) that mainly acts against the oxidative stress (Neill et al. 2002). However, at higher concentrations NO may prove to be potentially toxic to the plant systems (Lamattina et al. 2003). NO at elevated concentrations has an effect synergistic with that of ROS (Beligni and Lamattina 1999a, b).

As an important member of ROS, O_2^- has been shown to directly react with protein at Fe-S clusters, heme groups or S-S bonds and oxidize them (Thompson et al. 1987). Therefore O_2^- is devastating to electron transfer in photosynthesis. In the stroma of chloroplasts, the key enzyme of carbon metabolism, Rubisco is very sensitive to oxidative stress, causes cross-linking of large subunits at S-S (Mehta et al. 1992). O_2^- presumably mediates cell death symptoms (-apoptosis) including lipid peroxidation and subsequent membrane damage (Baker and Orlandi 1995). Metal ion sequestration as Fe and Cu by ferritin and Cu-binding proteins is thought to be important to prevent the formation of highly toxic OH^- via metal dependent Haber Weiss or Fenton reactions. Some of the highly toxic species' formation is prevented either through elevated expression of quenchers (reduced glutathione, ascorbic acid, proline etc.) or antioxidant enzymes (CAT, POX, SOD) viz. OH^-, singlet oxygen ($^1O_2$) etc. Anoxic stress leads to H_2O_2 formation plants cells. The level of H_2O_2 and O_2^- is maintained at steady state level through SOD, ascorbate peroxidase (APX), and/or CAT, since beyond their threshold they are toxic.

Hypoxic signals, perception and gene regulation

No oxygen sensor has yet been clearly identified in plants (Magneschi and Perata 2009). The expected candidates are haem or protein with haem cofactors (reviewed by Dat et al. 2004; Sairam et al. 2009). Class I hemoglobins (Hbs) maintain the low oxygen environment by tightly binding to the O_2 molecule. These non-symbiotic Hbs have been reported to be induced under hypoxia (Hunt et al. 2002) and shown to regulate the release of NO, therefore detoxifying their excess concentration. Recent proteomic and microarray analyses revealed the expression of more ANPs expressed temporally under various regimes of deprived O_2 in tomato, rice and *A. thaliana*. These include heat shock factors, ethylene responsive binding proteins (ERBP), MADS-box proteins, AP2 domain, leucine zipper, zinc finger, WRKY factors (Loreti et al. 2005; Lasanthi-Kudahettige et al. 2007), NIM1-like protein2, DWARF1 protein (BR biosynthesis), PAL, flavanone-3-hydroxylase (secondary metabolism), glutamyl t-RNA reductase1(porphyrin synthesis encoded by heme A gene; Tanaka et al. 1996), mtATPase α-subunit (Ahsan et al. 2007) alongwith several other well known ANPs belonging to enzymes of carbohydrate metabolism, glycolytic and fermentation pathways and aerenchyma formation.

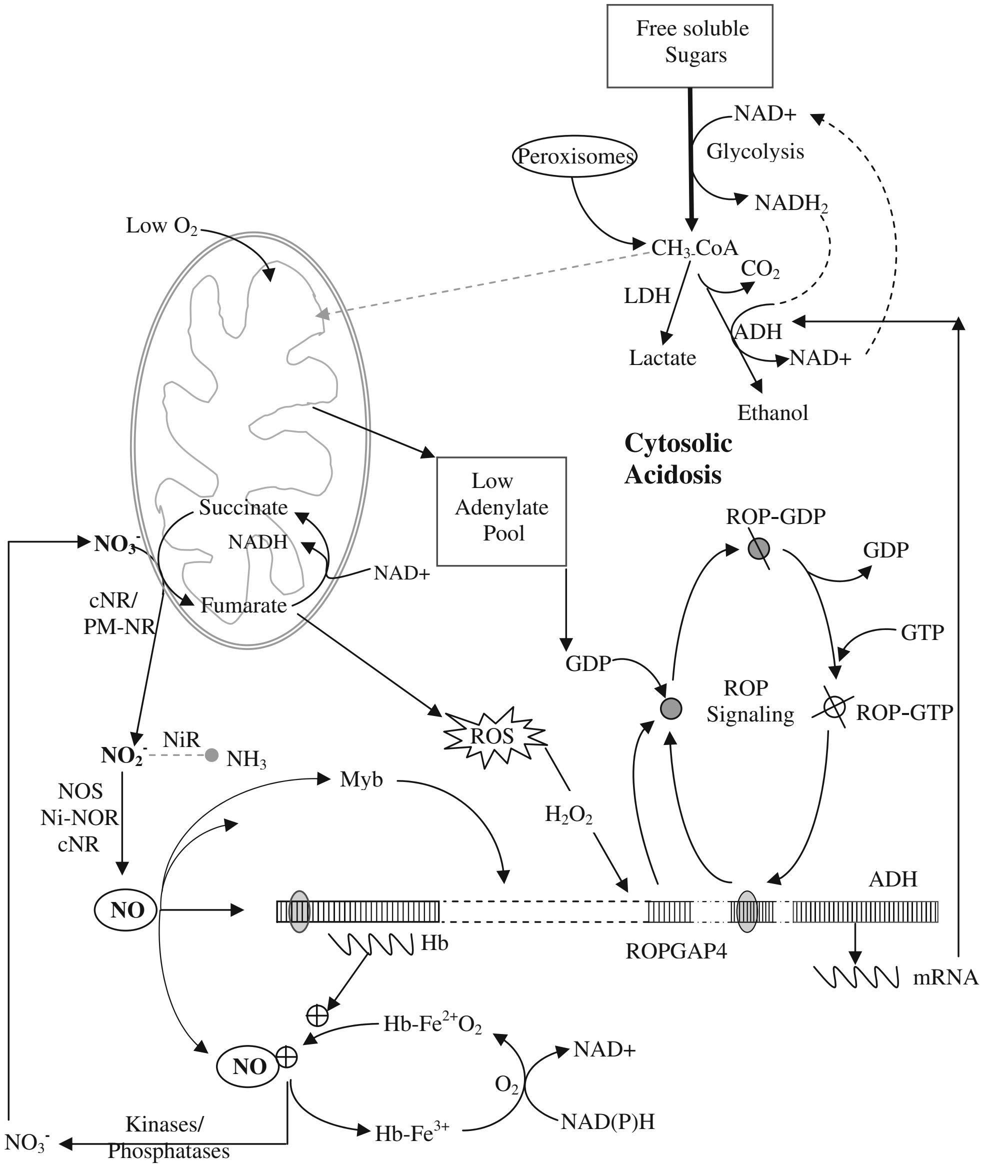
How plant (roots) sense depleting oxygen, is yet not clear. The role of ethylene in early singling is also elusive. However, efforts at molecular level revealed the identification of new cis-binding elements at promotor sequences and several trans-acting proteins. The work is still fragmentary and requires further investigations to resolve role of early signaling molecules and their working at initial level under influence of which roots switch to anaerobiosis. Recently identified ROP (Rho of Plants) G-proteins act as a molecular switch under hypoxic signaling (Fig. 1). ROP-GAP4 (ROP GTPase activating protein4) is a negative regulator of ROP signaling. ROPs is a GTP binding protein, promoted by hypoxia. The active ROP-GTP induces the expression and accumulation of mRNA encoding *adh* and ROPGAP4. Further the mutants defective in regulating the anaerobic induction of *adh* gene (aar1-1, aar1-2, and aar2-1) were identified. The formation of ROS has been noted in germinating rice seeds during normoxia and in *A. thaliana* and rice under hypoxia. ROS may secondarily produce H_2O_2 or other free radicals. Mutant study of ROP signaling indicated that H_2O_2 acts as both, positive and negative regulator. (Baxter-Burrell et al. 2002) proposed that production of signaling-competent ROS is mediated by ROP rheostat may provide tolerance to low oxygen management by regulating release of ROS and consumption of sugars (Fig. 1).

Also in part, the role of ethylene signaling in the hypoxic induction of *adh* was shown in *Arabidopsis* (Peng et al. 2001). However, proteomic analysis at early waterlogging sensing show expression of certain transcription factors may provide clues of promotor binding proteins up/down regulating the key enzymes of anaerobic pathways. Recently, several workers identified a new lot of ANPs with altered expression during early hypoxic conditions (Ahsan et al. 2007; Agarwal and Grover 2006). Some of these are even novel proteins, indicating their plausible roles in several other unknown mechanisms of defense operating at tissue specific manner.

Concluding remarks

The stress, in physiological sense; is state function, an altered condition caused by external factor(s) that tend to alter the equilibrium (Nilsen and Orcutt 1996) in plant. External cues plants may perceive as tissue specific manner. The sensitivity of sensing tissue determines the plant initial response to timely regulate its metabolism by the acclimation induction, up- or down-regulation of the expression of concerned genes/enzymes and their activity providing the ultimate resistance. The emergence of protein expression analyses spotted up-regulation of several ANPs during oxygen tension in the primary sensing tissues viz. germinating seeds, elongating coleoptiles, roots of seedlings and the root tips. Most of the up-regulated/induced proteins of ANPs, as shown, belong to the enzymes of carbohydrate metabolism (α-amylase, SuSy), glycolysis pathway (hexokinase, enolase, glyceraldehyde-3-phosphate dehydrogenase, phosphofructokinase, aldolase), (alcohol, lactic acid and alanine) fermentation pathways, nitrogen metabolism (GS, NR, NiR) with the additional proteins belonging to signaling (DWARF1, ACC synthase, ACC oxidase, NOS, CDPK), redox sensing (Hb, AsA, GSSG, POX, AOX, vacuolar and mtATPases), apoptosis (*xet*1,cys proteases), secondary metabolites (PAL, flavanone-3-hydroxylase), and transcription factors (WRKY, AtMyb2, MYB7) etc., while some others are suppressed (LDH, SAM, cys-desulfurase, PDH and BTF3 like transcription factors). Efforts to produce transgenic plants with upregulated expression of one or more of such key regulatory enzymes have been failed mostly. Researches switched over the regulation mechanisms of these enzymes at the conserved sequences of the promotors of abovementioned enzymes sharing the homology. The work on trans-acting binding factors revealed the role of ROP signaling and AtMyb transcription factor in regulating the battery of anaerobic genes under hypoxic conditions. The constitutive expression of AtMyb transcription factor, however, does not come up with success suggesting the constraints in the normal cellular metabolism by the constitutive induction of anaerobic genes under normoxia. A time-lapse study of expressions of ANPs, the analyses of involved transcription factors and their binding elements with sharing homologies with the promotor sequences of other ANPs will definitely add new insights understanding the gradual acclimation of root/plant under prevailing hypoxic/anoxic conditions. The over expression of early regulators (transcription factors) regulating recruitment/alteration of protein profile under hypoxia in transgenic plants with increased "copy number" under control of inducible promotor (instead of constitutive promotor) may lessen the metabolic constraint under normal oxygen/growth conditions but with added resistance, sensing upcoming oxygen stress.

Fig. 1 Production of nitric oxide, hemoglobin-nitric oxide cycle, and Rho of plants signaling regulation



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