

An Overview of Plant Responses to Soil Waterlogging

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ABSTRACT

Under natural conditions, plants are frequently exposed to transient or permanent soil waterlogging. Flooding drastically influences the soil physico-chemical properties, most notably soil redox potential, pH and O₂ level. Thus, conditions of hypoxia or anoxia are commonly encountered by plant root systems. These O₂ restrictive conditions dramatically affect plant growth, development and survival. One of the best characterised plant responses to soil waterlogging is the metabolic switch from aerobic respiration to anaerobic fermentation. In fact, most proteins induced during hypoxic conditions are enzymes involved in the establishment of this fermentative pathway. Because the plant cells need to keep a continuous ATP supply, the use of alternative electron acceptors and/or alternative pathways may be key elements of survival under soil waterlogging. The plant response may also include a reduction in stomatal conductance and photosynthesis, as well as root hydraulic conductivity. These physiological modifications may in turn affect carbohydrate reserves and translocation. In fact, efficient use of carbohydrates may discriminate between tolerant and intolerant species. Other observed adaptations include morphological changes which comprise the formation of hypertrophied lenticels, the initiation of adventitious roots and/or the development of aerenchyma. Our knowledge of the basic adaptive mechanisms of plants to soil waterlogging has benefited from large scale genomic and proteomic approaches, however, the diversity of the adaptive responses involved underlines the difficulty when studying this stress. This update reviews our current comprehension of the metabolic, physiological and morphological responses and adaptations of plants to soil waterlogging.

Keywords: anoxia, adaptation, hypoxia, roots, soil waterlogging

Abbreviations: ABA, abscisic acid; ADH, alcohol dehydrogenase; ANPs, anaerobic proteins; Eh, redox potential; Hb, hemoglobin; IAA, auxin; LDH, lactate dehydrogenase; Lp, hydraulic conductivity; NO, nitric oxide; PDC, pyruvate decarboxylase; PIPs, plasma membrane intrinsic proteins

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INTRODUCTION

Soil waterlogging has long been identified as a major abiotic stress and the constraints it imposes on roots have marked effects on plant growth and development. When such events take place in the spring, they can greatly reduce seed germination and seedling establishment. Thus, soil waterlogging is an important factor affecting the growth, development and survival of numerous plant species, not only in natural ecosystems but also in agricultural and horticultural systems (Dat *et al.* 2006).

Rapid changes in soil properties take place following soil waterlogging. As water saturates the soil pores, gases are displaced, a reduction in gas diffusion occurs and phytotoxic compounds accumulate as anaerobic conditions prevail. All these changes greatly affect the capacity of a plant to survive such conditions. In response, the stomatal resistance increases, photosynthesis and root hydraulic conductivity decline, and the translocation of photoassimilates is reduced.

However, one of the best characterised plant adaptations to hypoxia/anoxia includes a switch in biochemical and metabolic processes commonly observed when O₂ availability becomes limiting (Dat *et al.* 2004). The selective synthesis of a set of about 20 anaerobic stress proteins (ANPs) enables oxygen-independent energy generating metabolic processes under conditions unfavourable for aerobic energy production (Subbaiah and Sachs 2003). Other observed adaptations include morphological and anatomical changes which comprise the formation of hypertrophied lenticels, the initiation of adventitious roots and the development of aerenchyma (Vartapetian and Jackson 1997; Jackson and Colmer 2005; Folzer *et al.* 2006).

This review details the different plant stress responses to hypoxia/anoxia, induced by soil waterlogging/flooding and examines some of the key metabolic, physiological and morphological adaptive features.

CHANGES IN THE ROOT ENVIRONMENT DURING SOIL WATERLOGGING

As water saturates the soil, air spaces are filled, leading to the modification of several soil physico-chemical characteristics (Kirk *et al.* 2003; Dat *et al.* 2004). The first event that takes place is in fact the increased presence of H₂O: soil water saturation characterises flooding. Nevertheless, the mechanisms which trigger a plant response are often presumed by-products of root zone flooding (i.e. changes in soil redox and pH; a decline in O₂ level ...).

Soil redox potential (Eh) is often considered the most appropriate indicator of the chemical changes taking place during soil flooding (Pezeshki and DeLaune 1998). Eh generally declines during soil waterlogging (Pezeshki and DeLaune 1998; Pezeshki 2001; Boivin *et al.* 2002; Lu *et al.* 2004). It is not only an indicator of O₂ level (Eh around +350 mV under anaerobic conditions) (Pezeshki and DeLaune 1998) as reducing conditions lead to a high competitive demand for O₂, it also critically affects the availability and concentration of different plant nutrients (Pezeshki 2001). However, changes in Eh are influenced by the presence of organic matter as well as Fe and Mn (Lu *et al.* 2004). Soil reduction induces the release of cations and phosphorous through adsorption of ferrous ion and dissolution of oxides (Boivin *et al.* 2002). Soil reducing conditions also favour the production of ethanol, lactic acid, acetaldehyde and acetic and formic acid.

Another soil chemical characteristic which is strongly

affected by soil waterlogging conditions is soil pH, which is negatively correlated with Eh (Singh 2001; Zarate-Valde *et al.* 2006). The soil pH generally tends to increase towards neutrality upon waterlogging (Lu *et al.* 2004). The increase in pH may be explained by the dissolution of carbonate and bicarbonate early during waterlogging (Lu *et al.* 2004). Soil pH also affects the turnover of soil organic matter and processes such as mineralization, nitrification and urea hydrolysis (Probert and Keating 2000).

Overall, however, one of the main effects of flooding is a lower pool of available O₂ in the submerged plant part, as gases diffuse 10,000 faster in air than in water. The effect of O₂ limitation on cellular metabolism is concentration dependent and the gradual decline in O₂ availability in the root environment has varying effects on plant metabolism: i) normoxia allows aerobic respiration and metabolism to proceed normally and most of the ATP is generated via oxidative phosphorylation, ii) hypoxia occurs when the reduction in available O₂ starts to be a limiting factor for ATP production through oxidative phosphorylation and, iii) anoxia when ATP is only produced through fermentative glycolysis, as no more O₂ is available. Thus, as anaerobic conditions develop in the waterlogged soil, there is an increasing amount of by-products of fermentative metabolism accumulating in the root environment and the levels of CO₂, methane and volatile fatty acids increase (Pezeshki 2001). The decline in available energy has dramatic consequences on cellular processes, leading to water and nutrient imbalances and/or deficiency (Dat *et al.* 2006). In addition, these

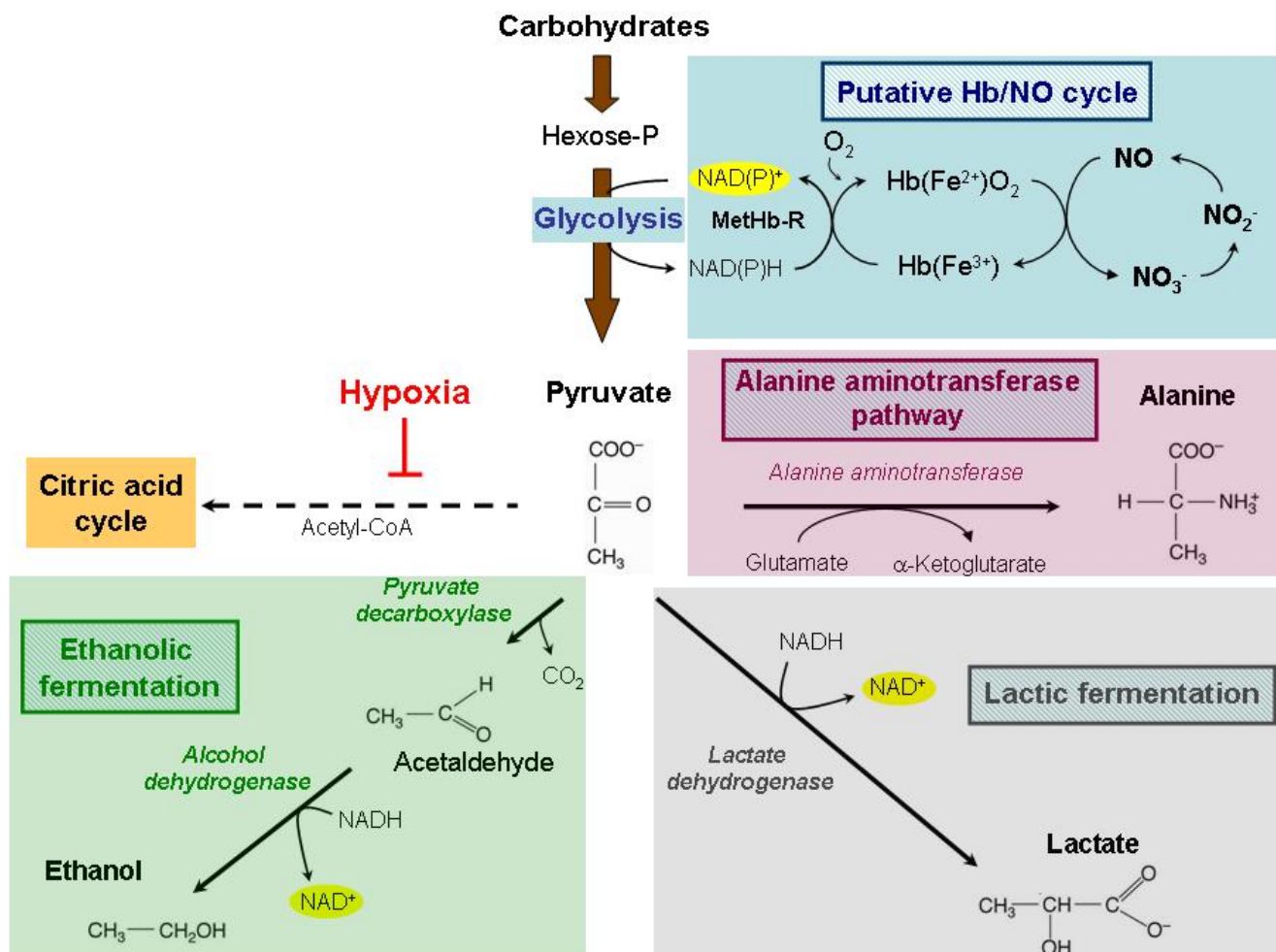


Fig. 1 Schematic diagram of the main metabolic pathways proposed during plant flooding stress. Hypoxia causes a decrease in mitochondrial respiration, which is partly compensated by increases in both the glycolytic flux and fermentation pathways. Nitrate has been proposed as an intermediate electron acceptor under low O₂ tensions and may participate in NAD(P)H oxidation during hypoxia (Igamberdiev *et al.* 2005). NO can be oxygenated to nitrate with the tightly bound O₂ of class-1 hemoglobin [Hb(Fe²⁺)O₂], which is oxidized to methHb [Hb(Fe³⁺)]. The alanine aminotransferase enzyme which converts pyruvate to alanine is strongly induced in hypoxic conditions. However, unlike ethanol formation, there is no consumption of NAD(P)H in the process (Gibbs and Greenway 2003). MetHb-R: methemoglobin reductase; NO: nitric oxide.

environmental changes may also make the plant more prone to other stresses, more particularly to pathogen infection (Munkvold and Yang 1995; Yanar *et al.* 1997; Balerdi *et al.* 2003).

METABOLIC RESPONSES AND ADAPTATIONS TO HYPOXIA AND ANOXIA

The immediate consequence of soil waterlogging is a period of hypoxia, followed by a strong decline in O₂ leading to anoxic conditions (Blom and Voeselek 1996). Indeed, cellular oxygen deficiency is termed “hypoxic” as soon as oxygen levels limit mitochondrial respiration and “anoxic” when respiration is completely inhibited. As respiration declines, the electron flow through the respiratory pathway is reduced, thus diminishing ATP production. Consequently, chemical oxidising power (i.e. nicotinamide adenine dinucleotide, NAD⁺) must be generated via alternative pathways that do not use O₂ as terminal electron acceptor (Roberts *et al.* 1984; Drew *et al.* 1994; Drew 1997; Summers *et al.* 2000). As adenosine diphosphate (ADP) oxidative phosphorylation becomes limiting, plants shift their metabolism from aerobic respiration to anaerobic fermentation (Fig. 1) (Peng *et al.* 2001; Fukao and Bailey-Serres 2004). The fermentative pathway serves as a metabolic safe route and includes two steps: carboxylation of pyruvate to acetaldehyde (catalysed by pyruvate decarboxylase, PDC) and the subsequent reduction of acetaldehyde to ethanol with concomitant oxidation of NAD(P)H to NAD(P)⁺, catalysed by alcohol dehydrogenase (ADH) (Vartapetian and Jackson 1997; Kingston-Smith and Theodorou 2000; Nakazono *et al.* 2000). The fermentative metabolic route allows the synthesis of only 2 moles of ATP against 36 per mole of glucose produced during aerobic respiration. To compensate the deficit in energy, glycolysis is accelerated, leading to the depletion of carbohydrate reserves (“Pasteur effect”). Not surprisingly, the enzymes that participate in the fermentation pathway (see above PDC and ADH) belong to a group of approximately 20 ANPs, selectively induced during hypoxic stress, whereas overall protein synthesis is reduced (Sachs *et al.* 1980; Chang *et al.* 2000). ANPs which are induced mainly under hypoxia include enzymes of glycolysis, ethanolic fermentation, processes related to carbohydrate metabolism but also others involved in aerenchyma formation (xyloglucans endotransglycosylase) and cytoplasmic pH control (Vartapetian 2006).

Species tolerant to soil waterlogging are generally considered those able to maintain their energy status via fer-

mentation. In addition to their ability to keep an appropriate energy level, maintenance of cytosolic pH is critical. When hypoxia or anoxia occur the pH of the cytoplasm shows an early decrease that is attributed to an initial production of lactic acid by fermentation. According to the “Davies-Roberts pH-stat theory”, the decline in pH permits the switch from lactate to ethanol fermentation by inhibition of lactate dehydrogenase (LDH) and activation of ADH (Chang *et al.* 2000). Because acidosis can induce cell necrosis, the switch taking place maintains pH at approximately 6.8, thus allowing cell survival. Although this hypothesis has been verified in some cases, there are numerous reports which question this model (Tadege *et al.* 1998; Kato-Noguchi 2000b). Indeed, it is obvious today that the correlation between lactate and cytoplasmic acidification is not ubiquitous in all tissues and plants studied (Felle 2005).

Because O₂ is lacking under hypoxic conditions, it has to be substituted by alternative electron acceptors. In fact, nitrate has long been considered as a terminal electron acceptor for plant mitochondria under hypoxic or anoxic conditions (Vartapetian and Polyakova 1998; Vartapetian *et al.* 2003). More recently nitrate reduction has been investigated as an alternative respiratory pathway, and it could be crucial for the maintenance of redox and energy homeostasis of the cell under limiting oxygen conditions (Igamberdiev and Hill 2004). This sequence of reactions, referred to as the Hb/NO cycle, in which NO (nitric oxide) is oxidized to nitrate, involves a class 1 non-symbiotic hemoglobin which is induced under hypoxia (Fig. 1) (Dordas *et al.* 2003; 2004; Perazzolli *et al.* 2004; Parent *et al.* 2008a). The postulated Hb/NO cycle was very recently demonstrated in hypoxic roots and in addition to being important during the plant flooding response it could also play a role early during seed germination (Hebelstrup *et al.* 2007).

PHYSIOLOGICAL RESPONSES TO SOIL WATERLOGGING

One of the earliest plant physiological responses to soil flooding is a reduction in stomatal conductance (Fig. 2) (Sena Gomes and Kozłowski 1980; Pezeshki and Chambers 1985; Folzer *et al.* 2006). Soil waterlogging may not only increase stomatal resistance but also limit water uptake, thus in term leading to internal water deficit (Jackson and Hall 1987; Ismail and Noor 1996; Pezeshki *et al.* 1996; Pezeshki 2001; Nicolas *et al.* 2005; Folzer *et al.* 2006; Parent *et al.* 2008a).

Low O₂ levels may also reduce hydraulic conductivity

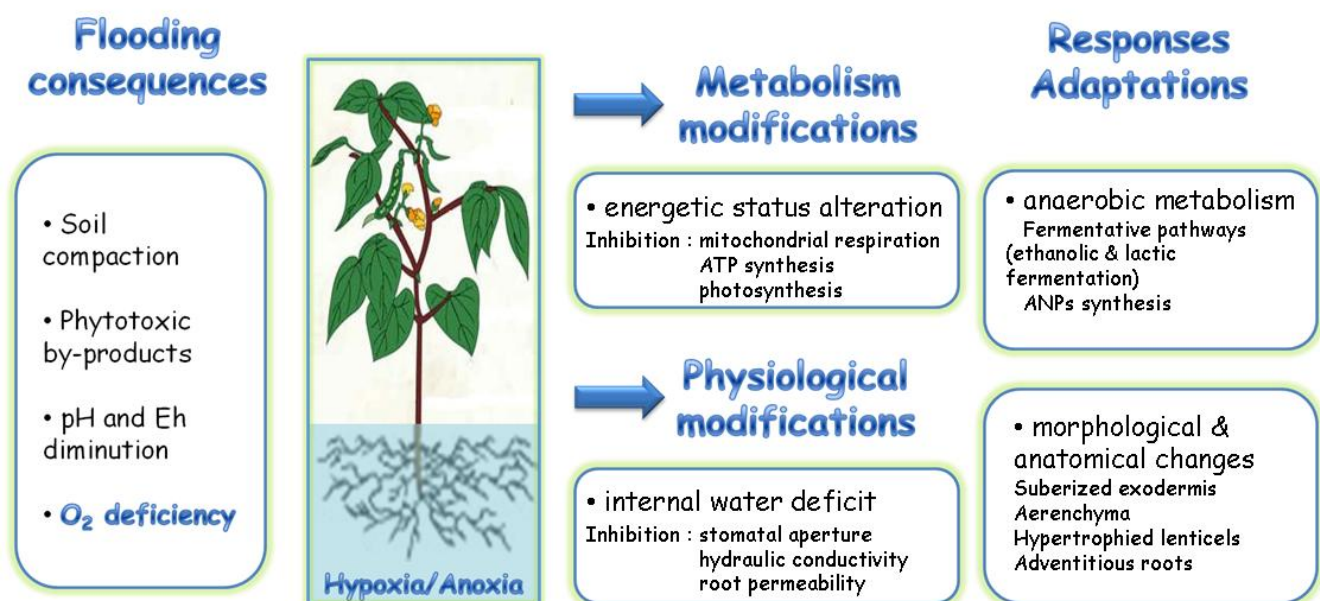


Fig. 2 Main physico-chemical events taking place in the rhizosphere during soil waterlogging and the resulting modifications in plant metabolism and physiology followed by the initiation of adaptive responses.

(Fig. 2; *Lp*) consequent to a decrease in root permeability (Clarkson *et al.* 2000; Else *et al.* 2001). The decrease in *Lp* may be linked to aquaporin gating by cytosolic pH (Tournaire-Roux *et al.* 2003). Evidence suggests that the regulation of plasma membrane intrinsic proteins (PIPs) by pH is especially relevant under anoxic conditions (Postaire *et al.* 2007), as a conserved histidine residue at position 197 in the intracellular Loop D has been identified to be the major pH-sensing site under physiological conditions (Tournaire-Roux *et al.* 2003; Kaldenhoff and Fischer 2006; Secchi *et al.* 2007). In fact, downregulation of aquaporin genes is commonly associated with a decline in root *Lp* as aquaporins control radial water movement in the roots (North *et al.* 2004; Vandeleur *et al.* 2005). Thus, it seems that the reduced *Lp* throughout the plant under soil waterlogging conditions is most probably linked to inhibition of water transport by aquaporins, though in depth studies on the effect of aquaporin on whole plant water regulation during soil waterlogging are still lacking. Furthermore, the reduction in radial water movement may in part be explained by the presence of cross-sectional oxygen gradients in the root tissue. Indeed, there is clear evidence that in flooded soils, an O_2 gradient exists between the stele, which may be under anoxic conditions, and the cortical cells which may only be under hypoxic conditions (Thomson and Greenway 1991; Colmer 2003). Thus, these differences in tissue microenvironment may also contribute to cross-sectional differences in cellular energy levels and subsequent declines in root *Lp*.

O_2 deficiency generally induces a rapid reduction in the rate of photosynthesis in flood-intolerant plants which is generally considered a result of reduced stomatal aperture (Huang *et al.* 1997; Gravatt and Kirby 1998; Pezeshki and DeLaune 1998; Malik *et al.* 2001). Other factors such as a decrease in leaf chlorophyll content, early leaf senescence and a reduction in leaf area may also contribute to inhibition of photosynthesis at a later stage (Sena Gomes and Kozlowski 1980; Cao and Conner 1999).

When the stress is prolonged it may lead to the inhibition of photosynthetic activity of the mesophyll (Huang *et al.* 1994; Liao and Lin 1994; Pezeshki *et al.* 1996), as well as reductions in the metabolic activity and the translocation of photoassimilates (Pezeshki 1994; Drew 1997; Pezeshki 2001; Sachs and Vartapetian 2007). The outcome of a decline in photosynthesis on plant growth and development

may be dramatic and it may lead to concurrent physiological dysfunctions such as the inhibition of water transport and changes in hormone balance (Vuylsteker *et al.* 1998; Kato-Noguchi 2000a; Else *et al.* 2001; Gunawardena *et al.* 2001). In order to maintain its metabolic activity, the plant has to draw on its carbohydrate reserves. As initial carbohydrate supply is correlated with the level of tolerance to hypoxia/anoxia in many species, presumably through its involvement in providing energy during anaerobic conditions, the level of carbohydrate reserves may be a crucial factor in the tolerance to long term flooding (Setter *et al.* 1997; Ram *et al.* 2002). For instance, an increased capacity to utilise sugars through the glycolytic pathway enables rice seedlings to survive longer periods of flooding (Ito *et al.* 1999).

Although a plant may have high sugar reserves, these must however be available and converted readily through an efficient glycolytic pathway. In fact, the availability of photoassimilates to the cells under anaerobiosis has been proposed as one of the limiting steps for survival under flooding conditions (Pezeshki 2001). Indeed, waterlogged soils tend to reduce the translocation of photosynthetic products from “source” leaves to “sink” roots (Barta and Sulc 2002; Yordanova *et al.* 2004). As a result, the maintenance of photosynthetic activity and accumulation of soluble sugars to roots is clearly an important adaptation to flooding (Chen *et al.* 2005).

MORPHOLOGICAL AND ANATOMICAL ADAPTATIONS TO SOIL WATERLOGGING

The presence of hypertrophied lenticels is a common anatomical change observed in many woody species during flooding (Fig. 3) (Yamamoto *et al.* 1995; Kozlowski 1997). Hypertrophic growth appears as swelling of tissues at the stem base and is believed to result from radial cell division and expansion. It has long been associated with auxin (IAA) and ethylene production (Blake and Reid 1981; Kozlowski 1997). The development of hypertrophied lenticels is believed to facilitate the downward diffusion of O_2 as well as the potential venting of compounds produced in the roots as by-products of anaerobic metabolism (ethanol, CH_4 , CO_2). Although there is still no clear consensus on their actual physiological role, their number has been associated with increase tolerance to flooding in *Quercus* species (Co-

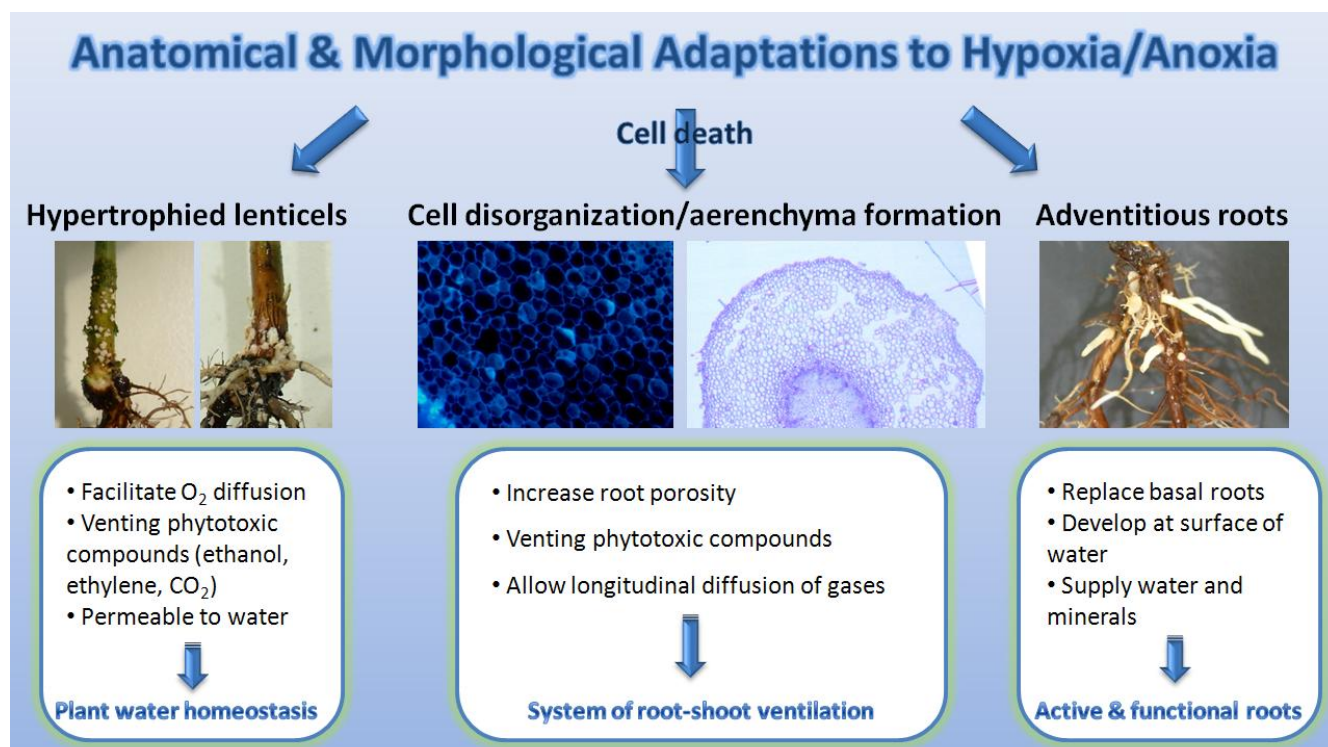


Fig. 3 Anatomical and morphological adaptations taking place during plant flooding.

lin-Belgrand *et al.* 1991; Parelle *et al.* 2006b). In addition, hypertrophied lenticels tend to be more developed under the water surface (Tang and Kozlowski 1982; Parelle *et al.* 2006a) which does not support a role as important facilitators of O₂ entry and delivery toward the root system, as commonly assumed. It is thus more probable that lenticels may in fact help maintain plant water homeostasis during flooding, by partially replacing the decaying root system and providing a means of water intake for the shoot. In support for such a role, lenticels are permeable to water (Groh *et al.* 2002), the tendency for stomatal conductance to return towards control levels after a transient decrease has generally been associated with their development (Pezeshki 1996; Gravatt and Kirby 1998; Folzer *et al.* 2006), and their presence is associated with maintenance of plant water status during flooding stress in *Quercus* species (Parent *et al.* 2008a). Thus, although their function is still not clearly established, it seems that lenticels may play a crucial role during adaptation to flooding conditions in some species by helping maintain shoot water homeostasis.

Another important morphological adaptation to flooding is the development of adventitious roots (**Fig. 3**), which functionally replace basal roots (Bacanamwo and Purcell 1999; Gibberd *et al.* 2001; Malik *et al.* 2001). The formation of these specialised roots takes place when the original root system becomes incapable of supplying the shoot with the required water and minerals (Mergemann and Sauter 2000). Furthermore, decay of the main root system may be considered as a sacrifice to allow a more efficient use of energy for the development of a more adapted root system (Dat *et al.* 2006).

Adventitious roots are commonly formed near the base of the stem or in the region where lenticels are abundant, and their growth is lateral, parallel to the water/soil surface. Their presence at the interface between the water saturated soil and atmosphere reflects their importance in replacing the normal root system both underwater and following retreat of the water table. Furthermore, the ability to produce adventitious roots is commonly associated with enhanced tolerance to flooding and their development has commonly been associated with ethylene production (Voeseinek *et al.* 1993; Mergemann and Sauter 2000; Steffens *et al.* 2006). More recently, other molecules have been identified as key players in their initiation (Pagnussat *et al.* 2002; 2003; 2004). Indeed, recent data indicate that NO production works downstream of IAA in the control of adventitious root formation. However, the understanding of the role of NO in the regulation of adventitious roots is in its infancy and important findings on the crucial role of NO in flooding stress tolerance may lie ahead.

Finally, one of the most important responses to waterlogging is the development of lacunae gas spaces (aerenchyma) in the root cortex (**Fig. 3**). The development of aerenchyma may be a response to flooding in both flood tolerant and flood intolerant species (Vartapetian and Jackson 1997; Schussler and Longstreth 2000; Chen *et al.* 2002; Evans 2004). On the other hand, aerenchyma formation is an adaptive response in flood tolerant species only, specifically in bottomland woody species (Kludze *et al.* 1994; Pezeshki 1996). The increase in porosity may enhance venting toward the shoot and the atmosphere of phytotoxic compounds, produced in the roots (i.e., ethanol, methane) (Visser *et al.* 1997; Visser and Pierik 2007) and/or enhance the longitudinal diffusion of gases in the roots, thus increasing their aeration (Laan *et al.* 1991; Evans 2004). In fact, the proportion of aerenchyma is generally considered as a key discriminating factor between wetland and non-wetland plants (Vasellati *et al.* 2001).

The development of aerenchyma or lacunae tissues is not unique to roots. They are also observed in the leaf sheath following submergence, forming an interconnecting system of shoot-root ventilation (Jackson and Armstrong 1999; Fabbri *et al.* 2005). Aerenchyma increases tissue porosity which itself can be initiated as a result of osmotic dependant changes in cell shape (**Fig. 3**) (Justin and Arm-

strong 1987; Folzer *et al.* 2006). The changes in cell shape and assemblage in the root cortex are most likely linked to enhanced cell wall loosening enzyme activity and with suberin deposition in the exodermis (Colmer 2003; De Simone *et al.* 2003; Armstrong and Armstrong 2005; Enstone and Peterson 2005).

The development of a suberized exodermis correlates with the development of aerenchyma in maize (Enstone and Peterson 2005) and is associated with a decline in radial loss of root O₂ (Visser *et al.* 2000; Armstrong and Armstrong 2005). Such a barrier on the periphery of the cortex may not only reduce the loss of O₂ to the rhizosphere but could also protect the plant from phytotoxins produced by microorganisms in the environment surrounding the roots (Soukup *et al.* 2002; Armstrong and Armstrong 2005; Soukup *et al.* 2007).

The development of aerenchyma has been investigated for many years and it is now clear that at least two types of developmental processes are involved. The first is the constitutive development of aerenchyma as it occurs whether or not the plant is under waterlogged conditions. It forms by cells separating during tissue development. The cell death type taking place through cell separating is termed schizogeny (formed by cell separation) and is developmentally regulated and independent of any external stimuli. It is the outcome of highly regulated tissue specific patterns of cell separation. The other type of cell death process is termed lysogeny (formed by partial breakdown of the cortex), resembles programmed cell death, typically observed during the hypersensitive response of plant pathogen interactions (Mittler *et al.* 1997; Parent *et al.* 2008b) and more recently identified during other abiotic stresses (Pellinen *et al.* 1999; Dat *et al.* 2001; Dat *et al.* 2003; Van Breusegem and Dat 2006). The active cell death process which takes place during aerenchyma development is genetically controlled and shows many similarities with apoptosis, though there is increasing evidence that it generally lacks several features of apoptotic cell death (Buckner *et al.* 2000). In *Sagittaria lancifolia* for example, nuclear changes (clumping of chromatin, fragmentation, disruption of the nuclear membrane), are the earliest events observed following flooding. These nuclear changes are followed by plasma membrane becoming crenulated, tonoplast disintegration, organelle swelling and disruption, loss of cytoplasmic contents and collapse of the cell (Schussler and Longstreth 2000). This sequence of events seems common to most species studied, though the timing of tonoplast disruption varies (Schussler and Longstreth 2000).

CONCLUSION

This short update reviews our current understanding of plant biochemical, physiological and morphological responses to soil waterlogging. The changes taking place in the root zone and their perception by the plant are clearly essential for the establishment of an appropriate response. The alteration in gas diffusion, the soil chemical environment (pH, Eh) and, the accumulation of toxic by-products of anaerobic processes coupled to the decline in O₂ are clearly keys to the capacity of a plant to set up the right response. These adaptive features include changes in metabolism which may help preserve the plant cell integrity. Although less efficient than aerobic processes, the fermentative pathway can help maintain the cell pH but also ATP homeostasis. In addition to the glycolytic pathway to lactate and to ethanol, nitrate reduction could be used as an alternative respiratory pathway to help maintain redox and energy homeostasis under hypoxic and anoxic conditions. Other features such as higher carbohydrate reserves and/or their efficient use, maintenance of photosynthesis and plant water status through shoot elongation or aquaporin gating may greatly improve plant survival to submergence. Finally, morphological changes such as lenticels formation, aerenchyma development, adventitious roots initiation and/or root suberization can not only ameliorate the rate of O₂ diffusion to the

submerged growing parts but also help alleviate water and nutrient deficiencies. Most of these adaptive features have been well characterised in model species adapted to flooding conditions such as maize, rice and *Carex*, however the exact role of lenticels as well as the molecular processes involved in aerenchyma formation still need further scrutiny. In addition, our understanding of the adaptive response of woody species making up forest ecosystems is still in its infancy.

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