Chapter 2
Waterlogging and Plant Nutrient Uptake

J. Theo M. Elzenga and Hans van Veen

Abstract Waterlogging affects several parameters that determine nutrient uptake from the soil by the roots. We checked systematically, for all the relevant parameters in the nutrient uptake model by Silberbush and Barber (Plant Soil 74:93–100, 1983), how waterlogging changes the magnitude of the parameter, changes that can be both positive and negative for nutrient uptake. If negative effects can be expected we also describe possible specific adaptive responses that could counter the negative effects on these parameters, of plants exposed to waterlogging. We conclude that although most flooding-tolerant species use a hypoxia-avoidance strategy (i.e. increase the supply of oxygen to the root tissue), increasing root length, facilitating infection by mycorrhizal fungi and modification of uptake kinetics could be used by plants to ameliorate the negative effect of flooding on nutrient uptake.

2.1 Introduction

Waterlogging occurs when the rate of infiltration of precipitation exceeds the combined rates of drainage and evaporation of a catchment or when floodwater submerges an area. Waterlogging has a dramatic impact on gas exchange and soil properties (Greenway and Gibbs 2003). Most plants are affected in a negative way by flooded conditions. Shoot and root nutrient content decreases (Ashraf and Rehman 1999; Khabaz-Saberi et al. 2006; Kuiper et al. 1994; Pang et al. 2007a) and carbon assimilation and transpiration are greatly reduced. (Ashraf and Rehman 1999; Kronzucker et al. 1998; Pezeshki 2001). When the ambient oxygen concentration is increased most of the effects of waterlogging are reduced

J.T.M. Elzenga (✉) and H. van Veen
Laboratory of Plant Physiology, Center for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14, Haren NL-9750AA, The Netherlands
e-mail: j.t.m.elzenga@rug.nl

S. Mancuso and S. Shabala (eds.), *Waterlogging Signalling and Tolerance in Plants*,
DOI 10.1007/978-3-642-10305-6_2, © Springer-Verlag Berlin Heidelberg 2010

(Kronzucker et al. 1998). Together with the observation that the effects of waterlogging can be reversed by supplying additional nutrients in the form of foliar sprays (Pang et al. 2007a) or ameliorated by application of nitrogen (Arnon 1937; Drew 1988), this suggests that hypoxia leads to severely reduced root functioning and nutrient uptake. The reduced nutrient uptake can be explained by changes that occur at a metabolic and cellular level. These effects are not only important from a fundamental perspective, but also have great relevance to agricultural.

Diffusion of gasses is 10,000 times slower in water than in air and thus in waterlogged soils gas exchange is severely impeded, which leads to a depletion of oxygen and an accumulation of carbon dioxide due to microbial and root respiration. Oxygen levels might drop within hours below the critical oxygen concentration (COC), a level at which the cell shifts from aerobic respiration to glycolysis. The efficiency of the glycolysis in generating ATP is much reduced compared to the aerobic mitochondrial respiration processes: 2 ATP/glucose versus ~38 ATP/glucose, respectively (Jackson and Ricard 2003; Huang et al. 2008). Upon oxygen depletion, some plant species respond by inducing pyruvate carboxylase and alcohol dehydrogenase and increase the rate of glycolysis (Summers et al. 2000; Dolferus et al. 2008). By accelerating glycolysis, plant cells produce at most 37% of the ATP produced under oxygen-sufficient conditions (Greenway and Gibbs 2003). Evidence is also being presented that under anoxic stress part of the metabolic processes shift from ATP as the energy source, to PPi during glycolysis (Huang et al. 2008). The reduction in ATP availability has strong repercussions for root development, root nutrient uptake and root maintenance.

One of the best-studied adaptations of plants to flooding conditions is the formation of aerenchymatic tissue in the root, which provides an alternative pathway for the supply of oxygen to the root tissue (Jackson and Armstrong 1999; Gibberd et al. 2001; Rubinigg et al. 2002). This requires that new, well-adapted, adventitious roots are formed (Visser et al. 1996). Radial oxygen loss is kept to a minimum so that the root tip becomes a well-oxygenated micro-climate (Jackson and Armstrong 1999). Most of the disadvantages for root metabolism imposed by the flooding-induced hypoxic conditions are thereby ameliorated. Plants that are not capable of increasing the oxygen supply through aerenchymous conducts in the root do face a more serious challenge.

In this review, we consider the effect of hypoxia and waterlogging on the nutrient supply of to the plant assuming that the respiration in the root tissue is seriously impaired and that the rhizosphere, the soil immediately surrounding the root is chemically reduced. The delivery of nutrient to the root surface is by either a) interception, the “bumping” of the growing root against the nutrient, b) mass flow, the transport to the root surface by the movement of water in the soil driven by processes such as percolation, transpiration and evaporation), and c) diffusion, the movement of a nutrient along a concentration gradient, which is often created by depletion of the nutrient by the root in the volume of soil in close proximity to the root surface. The rate of nutrient uptake depends on various anatomical, physiological, biochemical, chemical and physical processes in the root and the surrounding soil layer. For this chapter, we have adapted the analysis by Silberbush and Barber (1983, reprinted in Clarkson1985) of the relative effect of changes in the parameters in ion transport and uptake, as a guideline for our analysis. Fig. 2.1 is a graphical representation of this analysis. The parameters that were considered by Silberbush and Barber are:

K	Root elongation rate
r_o	Root diameter
r_i	Inter-root spacing
C_{li}	Initial nutrient concentration
D_e	Diffusion coefficient
B	Buffering strength
k_m	Affinity constant of nutrient uptake system
I_{max}	Maximal nutrient uptake rate
C_{min}	Minimal nutrient concentration that can be taken up from the medium
V_o	Transpiration rate (bulk water flow)

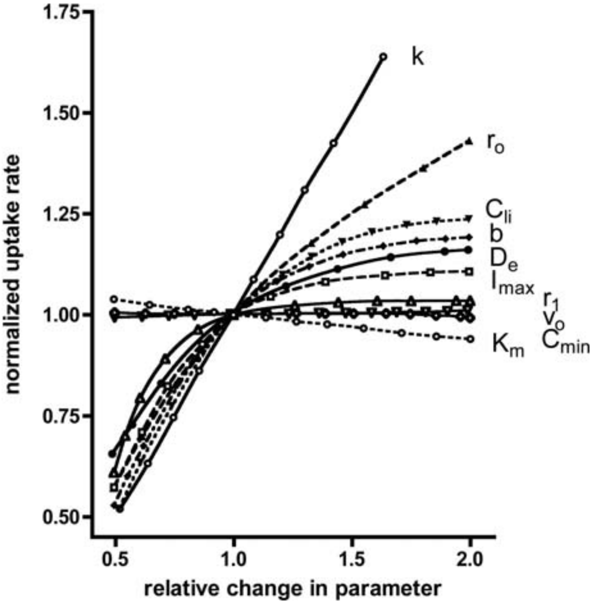

Fig. 2.1 Effects of changing the values of model parameters used for predicting phosphorus uptake by bean plants. It should be noted that the model sensitivity for changes in the parameters are could be strongly affected when the combination of starting values are chosen differently. The standard situation (change ratio = 1) is characterized by a rather high nutrient concentration and a wide spacing of competing roots. *k*: root elongation rate, r_o: root diameter, C_{li}: initial nutrient concentration, D_e: diffusion coefficient, *b*: buffering strength, k_m: affinity constant of nutrient uptake system, I_{max}: maximal nutrient uptake rate, C_{min}: minimal nutrient concentration that can be taken up from the medium, V_o: transpiration rate (bulk water flow), r_i: inter-root spacing. (After Silberbush and Barber 1983 as reprinted in Clarkson 1985)

The parameters k, r_o and r_i determine the general architecture of the root system and are essential for the "foraging capacity" of the plant. Foraging by the roots not only involves the utilization of mineral nutrients in the soil, but also applies to the uptake of water. The root system architecture together with the transpiration rate (bulk water flow), V_o, and the initial nutrient concentration, C_{li}, affects the effect of nutrient transport by mass flow. The diffusion coefficient and the buffering strength determine the diffusion of nutrients to the root surface. At the root surface, the uptake system of the plant, consisting of the transporter proteins in the plasma membrane that have specific properties with regard to maximal capacity, $I_{\max}$, affinity, k_m, and minimal nutrient concentration that can be taken up from the medium, $C_{\min}$, finally determines how efficiently the nutrients present at the plasma membrane of the root cortical cells are absorbed. In this chapter, we review our current knowledge how waterlogging affects the different parameters of the Silberbush and Barber analysis, and how plants can respond to these changes and in turn can modify these parameters by physiological, morphological or biochemical changes.

2.2 Effects of Hypoxia on Nutrient Uptake

2.2.1 Physiological Effects of Hypoxia Change Root Elongation Rate, k, and Maximal Nutrient Uptake Rate, $I_{\max}$

One of the immediate effects of flooding and hypoxia on the root physiology is the almost instantaneous arrest of root growth (e.g. Gibbs et al. 1998). The shift from aerobic respiration in the mitochondria to glycolytic generation of ATP does impose a serious reduction of available energy for the maintenance, growth and ion uptake. Although the specific allocation of respiratory cost to these different functions has not received much attention and different studies have yielded somewhat different figures, the consensus opinion is that about 20 to 45% of respiration is involved in growth (Veen 1981; Van der Werf et al. 1988; Poorter et al. 1991; Scheurwater et al. 1998; Scheurwater et al. 1999). Matching energy expenditure to energy generation would therefore demand that the investment of the plant in new root tissue is reduced. Root growth arrest could, however, also be the result of the accumulation of products of anaerobic metabolism. Self-poisoning could occur when protons accumulate in the cytoplasm and the vacuole and lead to a lethal drop in pH in the cytoplasm (Gerendás and Ratcliffe 2002). In *Phragmites australis* low molecular weight, volatile, monocarboxylic acids, like acetic acid, propionic acid, butyric acid and caproic acid, and sulphide, at concentration levels that have been measured in situ, arrested root elongation (Armstrong and Armstrong 2001). Specifically the application of a combination of these compounds was very effective and induced all the symptoms that are associated with root die-back. Sulphide, although it also can be used by the plant as sulphur source for the synthesis of cysteine and methionine, can act as a phytotoxin. In reduced soils the increased availability of ferrous iron and zinc can lead to accumulation in the plant to toxic levels (Pezeshki 2001).

In the analysis by Silberbush and Barber (1983), reduction of new root formation has a strong negative impact on potential nutrient uptake by reducing the interception of nutrients. The rate of root elongation, *k*, is one of the most important parameters determining the nutrient uptake rate. In more recent modelling excercises aimed at identifying important parameters for nutrient uptake, the foraging capacity, in which the elongation rate is an important factor, proved to be among the most essential properties of the root (e.g. Dunbabin 2006).

Controlled pot experiments have demonstrated that nutrient uptake is not only reduced through limited root growth, but that the uptake is also reduced on a per weight basis (Wiengweera and Greenway 2004; Kuiper et al. 1994). The allocation of respiratory cost to ion uptake is about 50 to 70% (Veen 1981; Van der Werf et al. 1988; Poorter et al. 1991; Scheurwater et al. 1998, 1999). Hypoxia can lead to a strong reduction in the adenylate energy charge (e.g. de Boer 1985; Sieber and Brandle 1991; Nabben 2001; De Simone et al. 2002). Reduction of the AEC can lead to a loss of the nutrient uptake capacity by limiting the supply of ATP to the plasma membrane proton pumping ATPase (de Boer 1985). As a consequence the membrane potential will become less negative and the proton gradient across the membrane will become less steep. Membrane potential and proton gradient form together the proton motive force, which is used to drive the uptake of most nutrients through symporters. It is indeed observed that upon anoxia the cytoplasmic pH drops from 7.4 to 6.9–7.1 and the plasma membrane becomes depolarized (Menegus et al. 1991; Xia and Roberts 1994). However, the possible causes for these effects are still under debate. Acidification could either be a negative by-product of glycolysis, lactic acid and high CO_2 accumulation, or be an adaptive change to optimize ethanol fermentation for energy production (Felle 2005). However, the high costs associated with lactic acid removal and the speed of the response suggests this is an adaptive response to switch to ethanol fermentation as soon as possible. But many adaptive traits to mitigate low pH are also up-regulated suggesting the opposite (Aurisano et al. 1995; Xia and Roberts 1994).

The depolarisation of the plasma membrane can also cause leakage of K^+ out of the cell by activating K^+ channels. In aged beet root disks the inhibition by 55% of Cl^- and K^+ uptake correlated, and was probably caused, by a decrease of the ATP concentration by 80% (Petraglia and Poole 1980). If lack of ATP supply to the plasma membrane ATPase is the cause of the reduction in nutrient acquisition, then nutrient uptake should be (partially) restored by stimulating ethanol fermentation by providing sufficient substrate. This mechanism has indeed been shown to function (Huang et al. 2008; Summers et al. 2000). However, several studies have shown that the anoxia-induced inhibition of nutrient uptake does not correlate with a reduction in the adenylate energy charge (Ishizawa et al. 1999) or with insufficient proton motive force (Zhang and Greenway 1995). These latter results indicate that inhibition of ion uptake is the result of down-regulation of transport systems. Although this down-regulation of the transport activity is not a direct, thermodynamic effect of the reduced synthesis of ATP, it is very likely that the down-regulation of transporter systems is part of the “energy saving” strategy of the plant, enabling the diversion of energy to even more essential processes like the regulation of cytoplasmic pH. A third possibility is provided by the results of Pang et al. (2007b) that show, that under oxygen-sufficient conditions the fermentation products of soil microbes under aerated conditions can mimic the effect of anoxia: membrane depolarisation and reduction of ion uptake.

2.2.2 Waterlogging Leads to Changes in the Availability, C_{li}, and the Effective Diffusion Coefficient, D_{e}, of Some of the Nutrients in the Soil

As oxygen is depleted soil microbes switch from using O_2 as an electron acceptor to NO_3^-, Fe^{3+} and Mn^{4+} leading to highly reduced conditions. Under severe waterlogging, SO_4^{2-} and CO_2 are also used in respiration (Gambrell and Patrick 1978, Madigan et al. 2003; Tiedje et al. 1984). More reduced conditions can lead to a lower availability of some plant nutrients, specifically nitrogen (Zhang et al. 1990). On the other hand at 100% field capacity the availability of the micronutrients Fe and Mn is strongly improved (Plekhanova 2007). An additional effect of waterlogging is that the phosphorus availability will also increase as result of Fe solubilization (Gambrell and Patrick 1978).

The denitrification as a result of nitrate respiration means that a substantial amount of nitrogen will be lost to the atmosphere as N_2, N_2O and NO (Gambrell and Patrick 1978; Madigan et al. 2003; Tiedje et al. 1984). When the soil chemistry leads to a reduced availability of nitrate, while simultaneously increasing the concentration of ammonia (Ashraf and Rehman 1999), this might have a beneficial effect on the budget of an energy deprived root system. It is assumed that the uptake of nitrate will cost the cell 1 ATP (1:1 stoichiometry of the H^+-NO_3^- symporter and a 1 H^+/ATP transported by the proton pumping ATPase). The subsequent assimilation of nitrate to glutamine consumes 12 ATP. The uptake of nitrogen from ammonia will partly be mediated by the diffusive passage of the membrane by NH_3, and not at the expense of a proton transported (although it should be noted that the acidifying effect of assimilation of ammonia will exacerbate the problem of cytoplasmic acidosis already caused by increased glycolytic activity). The assimilation into glutamine will only cost 2 ATP per ammonia. That in the flooding-sensitive beech (*Fagus sylvatica*) the NH_4^+ uptake is much less affected by flooding than NO_3^- (Kreuzwieser et al. 2002), and might be a consequence of the metabolic difference between these two N-compounds.

The water content of the soil has a pronounced effect on the effective diffusion coefficient D_{e} of plant nutrients. In soils with a volumetric water content of 0.40 g cm^{-3} only 10 μM P was necessary to achieve the same root uptake as compared with 200 μM P in a soil with a water content of 0.13 g cm^{-3}. For potassium the D_e increases from 2.55 to 4.91 to 6.40 × 10^{-7} cm^2 s^{-1} in soils with a water content of 0.19, 0.26 and 0.34 g cm^{-3}, respectively (Barber 1984). This effect of soil water content in ion uptake efficiency indicates that, particularly for phosphorus and potassium, a higher water saturation level of the soil has its advantages (Marschner 1995).

Due to the activity of sulphate reducing bacteria, sulphate will be depleted and high amounts of H_2S are produced under anoxic conditions in the pedosphere (Dassonville and Renault 2002). Sulphide can be taken up by the roots cells in analogy to the uptake of atmospheric H_2S through the stomata in the leaf mesophyll (Rennenberg and Polle 1994). Uptake of H_2S by the roots was demonstrated in *P. australis*. The potentially toxic H_2S was used for accumulation of thiols (Fuertig et al. 1996). In flooding tolerant poplar species the decreased allocation of reduced sulphur compounds from the shoot to the root and the accumulation of cysteine in the lateral roots indicated that the uptake of sulphide from reduced soils is a common process (Herschbach et al. 2005). Since the uptake of sulphide is energetically less expensive than the uptake of sulphate waterlogging is not expected to lead to S-deficiency.

2.2.3 In Waterlogged Conditions, Some Plant Species Show More Root Hair Development, Longer and Thinner Roots and Increased Levels of Infection With Mycorhizal Fungi – Effectively Increasing k

Plants have been shown to optimize their foraging strategy for water and nutrients. In a review by Bloom et al. (2003) it was shown that regulation by soil pH and redox potential of root cell division and mechanical properties result in root proliferation in nitrogen rich soil patches. In several studies with different species (tomato, mais) the pattern that emerges is that root growth is more enhanced when the available nitrogen is in the form of NH_4^+ than when it is only available as NO_3^-. Also plants develop thinner and longer roots when ammonium is the main nitrogen source, supposedly an appropriate strategy for scavenging a relatively immobile nutrient. From this example, it becomes clear that plants invest new biomass strategically and economically in structures with a long slender geometry. When roots are waterlogged growth is inhibited. One of the obvious reasons is that the high energy demand of growth cannot be met under anaerobic conditions. To deploy the limited resources under these conditions in an optimal way, would be to allocate them to the thinnest, longest structures possible, in order to maintain a high elongation rate.

Root hairs and mycorrhizal hyphae are thin structures associated with root functioning and presumably with the lowest carbon costs possible per volume of soil explored. To our knowledge no studies on the effects of waterlogging or hypoxia have been published. However, exposing roots to the ethylene precursor cyclopropane-1-carboxylate does, increase root hair formation in *Arabidopsis* roots

(Zhang et al. 2003; Schiefelbein 2000). The plant hormone ethylene is tightly related to flooding-adapted growth. Ethylene, being gaseous, diffuses at a more reduced rate in water than in air, leading to a quick accumulation upon flooding, and is a primary signal that activates water-adapted growth responses in Rumex palustris and deepwater rice (Visser and Voesenek 2004). Low phosphor in the growth medium can also increase higher root hair densities. The low P-induced root hair formation can be inhibited by adding ethylene inhibitors (Zhang et al. 2003). However, in most plants grown hydroponically root hairs are completely absent, caused by suppression of root hair initiation by the same plant hormone ethylene (Goormachtig et al. 2004).

The reported effects of waterlogging on colonization of roots by mycorrhizal fungi are similarly variable. In most publications fungal invection declines with the development of anaerobic conditions (Garcia et al. 2008) or that the increased availability of P under waterlogging depresses arbuscular mycorrhizal (AM) colonization (Stevens et al. 2002). In *Lotus tenuis,* the reduction in fungal infection was due to increased P availability and to a lesser extend to excess water (Garcia et al. 2008). Completely opposite results were found for AM infection in *Pterocarpus officinalis*. Flooded plants had well-developed mycorrhizas and plants that were infected were more flood-tolerant, having a higher growth rate and a higher P acquisition in the leaves (Fougnies et al. 2007). Also in *Casuarina equisetifolia* infected with *Glomus clarum* developed better when flooded than plants that were not infected (Osundina 1998). Ernst (1990) reported that mycorrhiza reduced the accumulation of toxic elements such as Mn and Fe. In *Panicum* and *Leersia* the infection or the roots by AM fungi was negatively affected by waterlogging, however, waterlogged plants that were colonized showed an improvement in phosphorus nutrition over non-colonized plants (Miller and Sharitz 2000). In a field survey that involved the same two grass species, AM colonization was strongly negatively correlated to the extent of waterlogging, but colonization was present in most root samples (Miller 2000). Although the focus has been on the effect of higher levels of phosphorus under waterlogged conditions on the infection rate, also other nutrients, like Zn, Fe and Cu, will be more available under waterlogging and precisely these elements have also been shown to be more readily available for plant roots that have an AM symbiosis (Fageria and Stone 2006). The combination of effects of waterlogging, hypoxia and increased nutrient availability, might partly explain the widely different results.

2.2.4 Waterlogging Decrease Evaporation and Bulk Water Flow, V_0

Many species show a reduction in the transpiration rate upon waterlogging (see Pezeshki 2001 for an overview). Control over the transpiration stream can occur anywhere along the pathway of water through the plant. The reported effects of waterlogging or hypoxia on the hydrolic conductivity of the root systems of different plant species have been summarized by Bramley (2006). Of the eight species listed, one species (*Agave deserti*) did not show a reduction in hydrolic conductivity, another species (*Lycopersicon esculentum*) did not respond in one study and showed a reduced hydrolic conductance in another, and in six species de hydrolic conductance was reduced. In *Arabidopsis* root, the anoxia-induced reduction in hydrolic conductance is the result of a conformational change of water channel proteins (aquaporins) when the cytoplasmic pH drops (Tournaire-Roux et al. 2003). In some plant species stomatal closure has been reported without significant changes in water status (Pezeshki 2001) leading to a reduction of the water flow through the plant, of 40% (Bradford and Hsiao 1982). Reducing the flow of water through the plant does reduce photosynthetic gas exchange and will reduce the nutrient supply to the root as it will decrease mass flow in the soil.

2.2.5 In Response to Waterlogging the Kinetics of Root Transport Systems, k_m and I_{max}, Can Be Modified

Only few studies are available where effects of waterlogging on the kinetic parameters of the root nutrient transport systems have been reported. In *Paspalum dilatatum*, a waterlogging-tolerant grass from South America, both the uptake capacity and the affinity of root transport system for phosphate were affected by waterlogging. The $V_{\mathrm{max},}$ of phosphate uptake increased by more than 100% on root weight basis. While the affinity significantly increases: the k_m was 42 µM under control conditions and 29 under waterlogging conditions (Rubio et al. 1997). This effect of waterlogging on *Paspalum dilatum* is different from rice where no effect of anoxia on P uptake capacity was found (John et al. 1974).

2.3 Summary and Concluding Remarks

Waterlogging has a severe effect on almost all the parameters that affect nutrient uptake from the soil. In Table 2.1 an overview of the effects of waterlogging on these parameters is presented, together with the possible adaptive responses of plants to counteract these effects. We purposely did not include the processes that will take place in rhizosphere of plants that form aerenchyma in the roots, providing a conduct for the transport of O_2 from shoot to root. In these plants most of the effects described above will be completely different: root function will be less affected and the redox potential of the rhizosphere will be much lower. The plants without aerenchyma in the roots generally can no longer use mitochondrial respiration to generate ATP and shift to glycolysis, while reducing energy demanding processes like growth and nutrient uptake. The cytoplasmic pH will become lower

Table 2.1 Summary of the effects of waterlogging on the root parameters used in the model described Silberbush and Barber. In the last column the possible functional adaptive response of roots which counteracts the effect of waterlogging is listed. The question mark following a response indicates that the functional response has only been described occasionally

Parameter		Effect of waterlogging	Functional response
k	Root elongation rate	Reduced	Formation of root hairs, association with AM fungi
r_o	Root diameter		Reduced
C_{li}	Initial nutrient concentration	Higher – lower	
D_e	Diffusion coefficient	Higher	
k_m	Affinity constant uptake system	No effect	Lowered?
I_{max}	Maximal nutrient uptake rate	Reduced	Increased?
C_{min}	Minimal nutrient concentration	No effect	
V_o	Bulk water flow	Reduced	

and hydrolic conductivity of the root will decrease due to acidosis. Stomata will close and the flow of water through the plant will be severely reduced. The production of volatile organic acids in the soil (maybe in combination with low ATP levels) leads to membrane depolarisation and die-back of root tips, resulting in much reduced root functionality. In the soil some nutrients become less available (N), or become available in another form (N, S), but for others (P, Fe, Zn) waterlogging improves their availability. In waterlogged soils also diffusion of mobile nutrients is increased. The literature on most of the possible adaptive responses is not unanimous. Reasons for this are the lack of a general model plant system, the variability in the conditions that are applied (hypoxia, anoxia, waterlogging, long adaptation periods, short exposures, etc.), but also an inherent lack of control over most of the variables involved. When soils are waterlogged a myriad of changes are induced and some of these changes will have opposite effects: waterlogging reduces root uptake capacity, but increase nutrient availability; nutrients become more readily available, but possibly to a toxic level.

But the lack of consensus is most probably another illustration of the fact that waterlogging-tolerance is not due to a single plant attribute, but to an amalgam of processes and features that enhance the survival of the plant.

References

Armstrong J, Armstrong W (2001) An overview of the effects of phytotoxins on *Phragmites australis* in relation to die-back. Aquat Bot 69:251–268

Arnon DI (1937) Ammonium and nitrate nutrition of barley at different seasons in relation to hydrogen ion concentrations, manganese, copper and oxygen supply. Soil Sci 44:91–113

Ashraf M, Rehman H (1999) Interactive effects of nitrate and long term waterlogging on growth, water relation and gaseous exchange properties of maize (*Zea mays* l.). Plant Sci 144:35–43

Aurisano N, Bertani A, Reggiani R (1995) Anaerobic accumulation of 4-aminobutyrate in rice seedlings: causes and significance. Phytochemistry 38:1147–1150

Barber SA (1984) Soil nutrient bioavailability. A mechanistic approach. Wiley, New York, USA

Bloom AJ, Meyerhoff PA, Taylor AR, Rost TL (2003) Root development and absorption of ammonium and nitrate from the rhizosphere. J Plant Growth Regul 21:416–431

Bradford KJ, Hsiao TC (1982) Stomatal behavior and water relations of waterlogged tomato plants. Plant Physiol 70:1508–1513

Bramley H (2006) Water flow in the roots of three crop species: the influence root structure, aquaporin activity and waterloggin. PhD Thesis, University of Western Australia

Clarkson DT (1985) Factors affecting mineral nutrient acquisition by plants. Annu Rev Plant Physiol 36:77–115

Dassonville F, Renault P (2002) Interactions between microbial processes and geochemical transformations under anaerobic conditions: a review. Agronomie 22:51–68

De Boer B (1985) Xylem/symplast ion exchange: mechanism and function in salt-tolerance and growth. Thesis, University of Groningen, Haren, The Netherlands

De Simone O, Haase JK, Mueller E, Junk WJ, Gonsior G, Schmidt W (2002) Impact of root morphology on metabolism and oxygen distribution in roots and rhizosphere of two Central Amazon flooding tree species. Funct Plant Biol 29:1025–1035

Dolferus R, Wolansky M, Carol R, Miyashita Y, Ismond K, Good A (2008) Functional analysis of lactate dehydrogenase during hypoxic stress in *Arabidopsis*. Funct Plant Biol 35:131–140

Drew MC (1988) Effects of flooding and oxygen deficiency on plant mineral nutrition. In: Lauchli A, Tinker PB (eds) Advances in plant nutrition. Praeger, New York, USA, pp 115–159

Dunbabin V (2006) Using the ROOTMAP model of crop root growth to investigate root-soil interactions. In: Turner NC, Acuna T, Johnson RC. Ground-breaking stuff. Proceedings of the 13th Australian Agronomy Conference, 10–14 Sept 2006, Australian Society of Agronomy, Perth, Western Australia

Ernst WHO (1990) Ecophysiology of plants in waterlogged and flooded environments. Aquat Bot 38:73–90

Fageria NK, Stone LF (2006) Physical, chemical and biological changes in the rhizosphere and nutrent availability. J Plant Nutr 29:1327–1356

Felle HH (2005) pH regulation in anoxic plants. Ann Bot 96:519–532

Fougnies L, Renciot S, Muller F, Penchette C, Prin Y, de Faria SM, Bouvet JM, Sylla SN, Dreyfus B, Ba AM (2007) Arbuscular mycorrhizal colonization and nodulation improve flooding tolerance in *Pterocampus officinalis* Jacq. seedlings. Mycorrhiza 17:159–166

Fuertig K, Ruegsegger A, Brunold C, Brandle R (1996) Sulphide utilization and injuries in hypoxic roots and rhizomes of common reed (*Phragmites australis*). Folia Geobotanica Phytotaxon 31:143–151

Gambrell RP, Patrick WH (1978) Chemical and microbiological properties of anaerobic soils and sediments. In: Hook RMM, Crawford C (eds) Plant Life in anaerobic habitats. Ann Arbor Science, USA

Garcia I, Mendoza R, Pomar MC (2008) Deficit and excess of soil water impact on plant growth of *Lotus tenuis* by affectig nutrient uptake and arbuscular mycorrhizal symbiosis. Plant Soil 204:117–131

Gerendás J, Ratcliffe RG (2002) Root pH regulation. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots – the hidden half, 3rd edn. Marcel Dekker, New York, pp 553–570

Gibberd MR, Gray JD, Cocks PS, Colmer TD (2001) Waterlogging tolerance among a divers range of *Trifolium* accessions is related to root porosity, lateral root formation and ‘aerotropic rooting’. Ann Bot 88:579–589

Gibbs J, Turner DW, Armstrong W, Darwent MJ, Greenway H (1998) Response to oxygen deficiency in primary maize roots. I. Development of oxygen deficiency in the stele reduces radial solute transport to the xylem. Aust J Plant Physiol 25:745–758

Goormachtig S, Capoen W, James EK, Holsters M (2004) Switch from intracellular to intercellular invasion during water stress-tolerant legume nodulation. PNAS (USA) 101:6303–6308

Greenway H, Gibbs J (2003) Mechanisms on anoxia tolerance in plants. II. Energy requirements for maintenance and distribution to essential processes. Funct Plant Biol 30:999–1036

Herschbach C, Mult S, Kreuzwieser J, Kopriva S (2005) Influence of anoxia on whole plant sulphur nutrition of flooding-tolerant poplar (*Populus tremula* x *P. alba*). Plant Cell Environ 28:167–175

Huang S, Colmer TD, Millar AH (2008) Does anoxia involve altering the energy currency to PPi? Trends Plant Sci 13:221–227

Ishizawa K, Murakami S, Kawakami Y, Kuramochi H (1999) Growth and energy status of arrowhead tubers, pondweed turions and rice seedlings under anoxic conditions. Plant Cell Environ 22:505–514

Jackson MB, Armstrong W (1999) Formation of aerenchyma and the processes of plant ventilation in relation to soil flooding and submergence. Plant Biol 1:274–287

Jackson MB, Ricard B (2003) Physiology, biochemistry and molecular biology of plant root systems subjected to flooding of the soil. In: de Kroon H, de Visser EJW (eds) Root ecology. Springer, Berlin, Heidelberg

John CD, Limpinuntana V, Greenway H (1974) Adaptation of rice to anaerobiosis. Aust J Plant Physiol 1:513–520

Khabaz-Saberi H, Setters TL, Waters I (2006) Waterlogging induces high to toxic concentrations of iron, aluminum and manganese wheat varieties on acidic soil. J Plant Nutr 29:899–911

Kreuzwieser J, Fuerniss S, Rennenberg H (2002) Impact of waterlogging on the N-metabolism of flood tolerant and non-tolerant tree species. Plant Cell Environ 25:1039–1049

Kronzucker HJ, Kirk GJD, Siddiqi MY, Glass ADM (1998) Effects of Hypoxia on $^{13}NH_4^+$ fluxes in rice roots, kinetics and compartmental analysis. Plant Physiol 116:581–587

Kuiper PJC, Walton CS, Greenway H (1994) Effects of hypoxia on ion uptake by nodal and seminal wheat roots. Plant Physiol Biochem 32:267–276

Madigan MT, Martinko JM, Parker J (2003) In: Brock (ed) Biology of microorganisms. Prentice Hall, London, UK

Marschner H (1995) Mineral nutrition of higher plants, 2nd edn. Academic, London, p 889

Menegus F, Cattaruzza L, Mattana M, Beffagna N, Ragg E (1991) Response to anoxia in rice and wheat seedlings. Plant Physiol 95:760–767

Miller SP, Sharitz RR (2000) Manipulation of flooding and arbuscular mycorriza formation influences growth and nutrition of two semiaquatic grass species. Funct Ecol 14:738–748

Miller SP (2000) Arbuscular mycorrhizal colonization of semi-aquatic grasses along a wide hydrological gradient. New Phytol 145:145–155

Nabben RHM (2001) Metabolic adaptations to flooding-induced oxygen deficiency and post-anoxia stress in Rumex species. Thesis, Utrecht University, Utrecht, The Netherlands

Osundina MA (1998) Nodulation and growth of mycorrhizal *Casuarina equisetifolia* J.R. and G. First in response to flooding. Biol Fertil Soils 26:95–99

Pang J, Ross J, Zhou M, Mendham N, Shabala S (2007a) Amelioration of detrimental effects of waterlogging by foliar nutrient spray in barley. Funct Plant Biol 34:221–227

Pang JY, Cuin T, Shabala L, Zhou M, Mendham N, Shabala S (2007b) Effect of secondary metabolites associated with anaerobic soil conditions on ion fluxes and electrophysiology in barley roots. Plant Physiol 145:266–267

Petraglia T, Poole RJ (1980) Effect of anoxia on ATP levels and ion transport rates in red beet. Plant Physiol 65:973–974

Pezeshki SR (2001) Wetland plant responses to soil flooding. Environ Exp Bot 46:299–312

Plekhanova IO (2007) Transformation of Fe, Mn, Co and Ni compounds in humic podzols at different moisture. Soil Biol 34:67–75

Poorter H, Van der Werf A, Atkin OK, Lambers H (1991) Respiratory energy requirements of roots vary with the potential growth rate of a plant species. Physiol Plant 83:469–475

Rennenberg H, Polle A (1994) Metabolic consequences of atmospheric sulphur influx into plants. In: Alscher RG, Wellburn AR (eds) Plant responses to the gaseous environment. Chapman and Hall, London, UK, pp 165–180

Rubinigg M, Stulen I, Elzenga JTM, Colmer TD (2002) Spatial patterns of radial oxygen loss and nitrate net flux along adventitious roots of rice raised in aerated or stagnant solution. Funct Plant Biol 29:1475–1481

Rubio G, Oesterheld M, Alvarez CR (1997) Lavado RS Mechanism for the increase in phosphorus uptake of waterlogged plants: soil phosphorus availability, root morphology and uptake kinetics. Oecologia 112:150–155

Scheurwater I, Cornelissen C, Dictus F, Welschen R, Lambers H (1998) Why do fast-and slow-growing grass species differ so little in their rate of root respiration, considering the large differences in rate of growth and ion uptake? Plant Cell Environ 21:995–1005

Scheurwater I, Clarckson DT, Purves JV, Van Rijt G, Saker LR, Welschen R, Lambers H (1999) Relatively large nitrate efflux can account for the high specific respiratory costs for nitrate transport in slow-growing grass species. Plant Soil 215:123–134

Schiefelbein JW (2000) Constructing a plant cell. The genetic control of root hair development. Plant Physiol 124:1525–1531

Sieber M, Brandle R (1991) Energy metabolism in rhizomes of *Acorus calamus* L. and in tubers of *Solanum tuberosum* L. with regard to their anoxia tolerance. Bot Acta 104:79–282

Silberbush M, Barber SA (1983) Sensitivity of simulated phosphorus uptake to parameters used by a mechanistic mathematical model. Plant Soil 74:93–100

Stevens KJ, Spender SW, Peterson RL (2002) Phosphorus, arbuscular mycorrhizal fungi and performance of he the wetland plant *Lythrum salicaria* L. under inundated conditions. Mycorrhiza 12:277–283

Summers JE, Ratcliffe RG, Jackson MB (2000) Anoxia tolerance in the aquatic monocot *Potamogeton pectinatus*: absence of oxygen stimulates elongation in association with unusually large Pasteur effect. J Exp Bot 52:1423–1422

Tiedje TM, Sexstone AJ, Parkin TB, Revsbech NP, Shelton DR (1984) Anaerobic processes in soils. Plant Soil 76:197–212

Tournaire-Roux C, Sutka M, Javot H, Gout E, Gerbeau P, Luu D-T, Bligny R, Maurel C (2003) Cytosolic pH regulates root water transport during anoxic stress through gating of aquaporins. Nature 425:393–397

Veen BW (1981) Relation between root respiration and root activity. Plant Soil 63:73–76

Visser EJW, Bogemann GM, Blom CWPM, Voesenek LACJ (1996) Ethylene accumulation in waterlogged *Rumex* plants promotes formation of adventitious roots. J Exp Bot 47:403–410

Visser EJW, Voesenek LACJ (2004) Acclimation to soil flooding – sensing and signal-transduction. Plant Soil 254:197–214

Wiengweera A, Greenway H (2004) Performance of seminal and nodal roots of wheat in stagnant solution: K+ and P uptake and effects of increasing O_2 partial pressures around the shoot on nodal root elongation. J Exp Bot 55:2121–2129

Van der Werf A, Kooijman A, Welschen R, Lambers H (1988) Respiratory energy costs for the maintenance of biomass, for growth and for ion uptake in roots of *Carex diandra* and *Carex acudformis*. Physiol Plant 72:483–491

Xia JH, Roberts JKM (1994) Improved cytoplasmic pH regulation, Increased lactate efflux, and reduced cytoplamsic lactate levels are biochemical traits expressed in root tips of whole maize seedlings acclimated to a low oxygen environment. Plant Physiol 105:651–657

Zhang B-G, Puard M, Couchat P (1990) Effect of hypoxia, acidity and nitrate on inorganic nutrition in rice plants. Plant Physiol Biochem 28:655–661

Zhang Q, Greenway H (1995) Membrane transport in anoxic rice coleoptiles and storage tissues in beetroot. Aust J Plant Physiol 22:965–975

Zhang Y-J, Lynch JP, Brown KM (2003) Ethylene and phosphorus availability have interacting yet distinct effects on root hair development. J Exp Bot 54:2351–2361