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Annual Review

GEOCHEMICAL PROCESSES AND NUTRIENT UPTAKE BY PLANTS IN HYDRIC SOILS

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Abstract—Soil reduction caused by flooding has profound effects on species adaptation and mineral nutrition of higher plants. Anaerobic conditions inhibit normal root respiration of higher plants. Alternate metabolic pathways may be utilized in combination with the development of anatomical characteristics that result in the internal movement of oxygen to the roots. Soil organisms use other oxidants when the oxygen supply is interrupted, which results in profound changes in oxidative states of many metals and nonmetals, and changes in soil reaction and conductivity. The products of reduction are primarily nitrogen gas, manganous manganese, ferrous iron, sulfide sulfur, methane, and organic acids. These reduction products alter the availability of soil nutrients and can drastically alter the soil acidity. Plant–soil interactions on flooded soils can sometimes be altered, as has been demonstrated by the use of phosphorus fertilizer on southern pine and zinc on rice.

Keywords—Soil reduction Plant anoxia Mineral nutrition Plant metabolism
Wetland soil–plant interactions

INTRODUCTION

Hydric soils are often characterized as highly productive because they usually contain ample moisture and nutrients. Their productive potential is limited, however, by the availability of O_2 during periods of inundation that are typical of hydric soils. Chemically reduced conditions quickly develop under soil waterlogging. The frequency and duration of events determine which plants will grow on these sites and their potential uses. Hydric sites also have enormous potential as sinks and as filters of certain pollutants, such as NO_3^- [1]. However, they may be especially sensitive to other pollutants, such as reducible metals. An understanding of the basic chemistry of frequently flooded soils is essential for maintaining the productivity and diversity of wetland ecosystems.

In this paper, we will outline the changes that occur in soils as they are reduced by flooding and the responses of plants to these changes. We will also examine how hydric sites can be managed for optimum productivity of well-adapted species. For additional information on soil chemistry, we recommend Buol and Rebertus [2], Ponnamperuma [3], Gambrell and Patrick [4], Gilmour and Gale [5], Hosner and Baker [6], and Stepniewski and Glinski [7]. Books edited by Kozlowski [8] and Hook and Crawford [9] are excellent sources of information on plant responses to hypoxia.

SOIL PHYSICAL CHARACTERISTICS

In most arable soils, O_2 is present throughout the profile occupied by plant roots. However, the partial pressure of O_2 is generally lower and that of CO_2 generally higher than in the aboveground atmosphere. The fluxes of these gases are controlled by a number of physical factors, including porosity of the soil and, more important, changes in temperature and moisture [10]. Temperature is important because it controls the solubility of gas in water. Appreciable amounts of gas are exchanged by conductance in the water component of the soil. Conductance is particularly important where water is moving through the soil profile.

When the soil is inundated, the movement of gases is severely decreased. Stepniewski and Glinski [7] indicate that gas exchange in the saturated soil profile is slower than in aerated soils by a factor of about 300,000. As soil organisms consume O_2, the composition of the dissolved gases changes drastically. Carbon dioxide concentrations increase to the point where this gas composes most, if not all, of the gas phase of the system. This change takes place in 1 to 3 d, depending on the biological activity of the soil or sediment profile [3].

At the soil surface, a transition zone exists where downward O_2 diffusion exceeds O_2 consumption

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by organisms. This zone is normally not more than 1 to 3 cm deep [11]. As with other aspects of hydric soils, depth of the transition zone depends on biological activity in the soil. Interestingly, lake sediments also have an oxidized layer on the surface of the sediment similar to the transition zone of hydric terrestrial soils. The uniformity of the transition zone in inundated areas depends partially on vegetation and penetration of light to the sediment surface. As we will discuss later, vegetation can transport limited amounts of O_2 into hydric soils.

The depletion of O_2 in cultivated hydric soils appears to be homogeneous. That is, O_2 loss is fairly uniform throughout the plowed or cultivated portion of the soil profile, such as in rice soils. In uncultivated hydric soils, O_2 depletion is more heterogeneous. Plant residues and plant roots are distributed unevenly over an uncultivated site. Under these conditions, organic matter, which is the energy source for soil reduction, tends to be concentrated at the soil surface. Hence, O_2 depletion tends to be more rapid close to the surface (10 cm from the surface compared to 20 cm) (W.H. McKee, unpublished data).

SOIL NUTRIENT REACTIONS

Under aerobic conditions, organisms respire by passing electrons to O_2, which forms oxides mainly with C. In the absence of O_2, facultative organisms can carry on respiration by passing electrons to alternate electron acceptors. As the O_2 in the microorganisms' environment is depleted, other oxidants are used in the order of their ease of reduction. The order is NO_3^-, Mn^{4+}-Mn, Fe^{3+}-Fe, SO_4^{2-}-S, and reducible C, which forms CH_4. The process by which anaerobic respiration takes place is referred to as an *oxidation-reduction* (redox) reaction, in which electrons are transferred from a donor to an acceptor. The unit of measure for quantifying the state of oxidation-reduction in soils is termed *redox potential* (Eh) and measured in volts. Values of 0.8 to 0.4 V are considered characteristic of aerated soils, whereas values in the range of 0.2 to −0.2 V are considered representative of reduced soils [4]. The intensity of reduction in these anaerobic environments also depends on the acidity of the solution. The intensity of reduction increases 0.0592 V for each drop of one unit pH [3]. Thus, for the redox potential to have meaning, it must be expressed in terms of a uniform pH value or it must be combined with the pH in a single expression. Combining is done by dividing the redox potential value by 0.0592 V (Nernst slope) to obtain the value pe, which is added to pH (pe + pH) [12]. Using Gambrell and Patrick's [4] values, soils with an Eh below 0.3 V at pH 7, which is comparable to a pe + pH of 12, are considered anaerobic. Values <12 indicate reduced conditions, and values >12 indicate oxidized conditions.

When oxides serve as electron acceptors, increases in the intensity of soil reduction cause significant changes in the nature of the soil solution (Fig. 1, adapted from Langdon and McKee [13]). However, there is generally an increase in the pH of the soil solution independent of the redox potential on acid soils and, after several weeks, a slight decrease in pH [12]. Drainage of the soil and subsequent reoxidation reverse this process. The pH effect will be further discussed in relation to Fe reduction.

Upon saturation, the O_2 in the soil is rapidly consumed and the CO_2 content of the soil increases because of very slow gas diffusion. The CO_2 production is suppressed at the lower redox state, because it is more difficult for organisms to respire. The order of electron acceptor reaction, as indicated above, is sequential relative to the position of the ions on the electromotive series [14]. Theoretically, the total content of each ion is consumed before the next ion on the series is used, but there may be simultaneous reduction of ions with similar redox potentials. After free O_2 is consumed, NO_3^- ions are the first electron acceptors where NO_3^- is reduced to N_2. Nitrite, an NO_3^- reduction intermediate, has been shown to be toxic to the roots of some plant species [15]. Ammonium is the primary source of soil N for plants in a reduced soil [16]. Following the reduction of NO_3^-, Mn^{4+}-Mn is reduced to Mn^{2+}-Mn. The reduction of Mn increases the solubility of the metal, and the ion becomes an important part of the soil solution. Following the reduction of Mn, Fe^{3+}-Fe is reduced to Fe^{2+}-Fe.

This reaction has strong implications in hydric soils because carbonate complexes of Fe are frequently present. The reduction of Fe coincides with a marked change in soil pH. If sufficient Fe is present, acid soils become neutral. In contrast, alkaline soils tend to become more acid with HCO_3^- formation. The equilibrium point for this relationship is a pH of 6.8. The pH change is due in part to the amphoteric property of Fe and the introduction of significant quantities of a soluble cation. Also, the reduction process itself either produces OH^- or consumes H^+, theorized as follows [3]:

$$Fe(OH)_3 + H^+ \rightarrow Fe(OH)_2 + H_2O$$

oxidized reduced

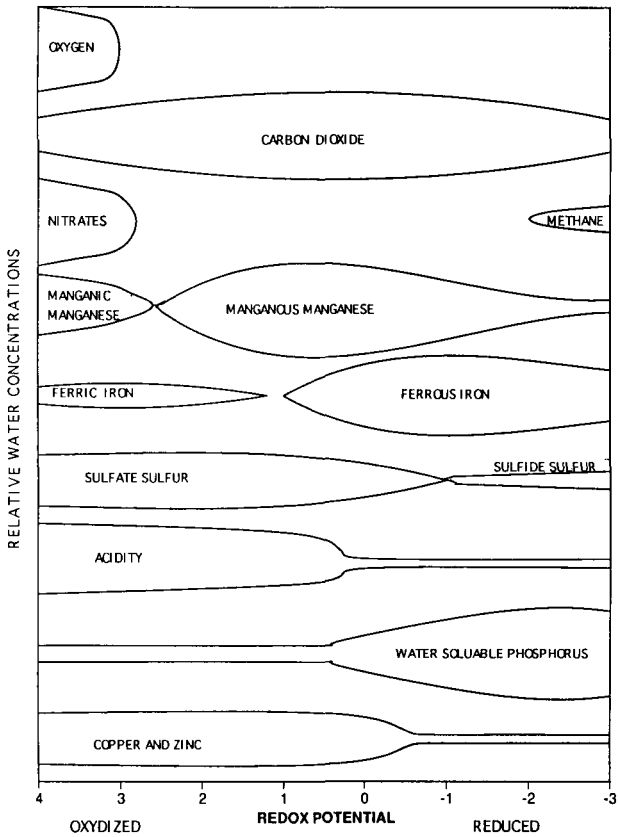

Fig. 1. Changes in relative concentrations of soil nutrients with waterlogging. Negative redox potentials indicate a high degree of waterlogging. Adapted from Langdon and McKee [13].

When a soil is drained, this reaction is reversed and the soil pH returns to its previous acid state. Repeated oxidation and reduction of soils slowly solubilize the Fe, leaving a gley or gray color that indicates a relative lack of drainage. Iron toxicity and, in a few instances, Mn toxicity to plants have been reported [17,18]. Waterlogging tolerance is often evaluated with respect to the ability of a plant to inhibit excessive Fe and, in some cases, Mn uptake [19–21].

After soil Fe is reduced, microorganisms are able to reduce SO_4^{2-} to S^{2-} at a redox potential of approximately −0.10 V. The presence of this reaction is indicated by the odor of H_2S. Sulfide has a mixed effect on higher plants. Sulfide is toxic to plants, but the ion readily reacts with many equally toxic heavy metals, removing them from the soil solution [22]. Hydrogen sulfide precipitates Fe, Zn, Cu, and Cd, which become less available due to the formation of insoluble metal sulfides [3,4,23]. The presence of large amounts of S^{2-} in organic marsh soils where FeS has accumulated as pyrite poses special problems. If these soils are drained, the S^{2-} oxidizes and forms H_2SO_4, reducing pH values to below 2. This type of soil is often called "cat clay" [24].

Under extremely reduced soil conditions, free S^{2-} concentration in the soil solution can reach very high levels, and even tolerant plant species lack the oxidizing ability to reoxidize S^{2-} to SO_4^{2-} in the rhizosphere [3]. Under these conditions, FeS may precipitate at the root surface on previously formed Fe plaques, temporarily preventing excessive uptake of both Fe and S^{2-}. However, once the Fe oxides are reduced, S^{2-} can enter the plant nonselectively. Excessive S^{2-} accumulation has been linked to loss of cytochrome oxidase activity in moderately tolerant and intolerant species [25].

The final electron acceptor of soil reduction is CO_2, which is transformed into CH_4 (swamp gas).

This reaction proceeds when all other electron acceptors have been reduced and sufficient organic matter is present for consumption by microorganisms.

Aluminum makes up a large portion of the amorphous component of hydric mineral soils, but the energy required for Al reduction is sufficiently high to prevent its reduction. The relatively high pH in flooded soils prevents exchangeable Al ions from entering solution in weathered acid soils [26]. If such soils are drained, acidity increases tremendously, and Al can enter the solution. This ion is toxic to many plants through disassociation of the hydrated Al_2O_3.

The effects of redox on availability of nonreducible plant nutrients are also important. Phosphorus has received considerable attention, especially in the culture of rice. In rice soils, when Fe is reduced in $Fe_3(PO_4)_2$ minerals, P is solubilized; the reaction is reversed when the soil is drained [4]. Sah et al. [27] found that the availability of P upon flooding depends on levels of reducible Fe and organic matter. Organic matter levels below 8 g/kg were insufficient to increase P availability.

Woody species, such as loblolly and slash pine, respond to applied P on wet sites but not on moderately well-drained sites when the same levels of residual P are present in the soil [28], the result of a change in plant physiology more than nutrient availability, which is discussed later. On hydric soils, such as peats, P can be rendered unavailable through formation of organic P compounds [29]. Based on thermodynamic predictions, mineral soils with low Fe and high exchangeable Al levels can precipitate P into extremely insoluble minerals such as vivianite [12].

In lake and stream sediments, soluble P may exist in the reduced zone below the surface of sediments. The soluble P in the sediments will not contaminate the overlying water unless the thin oxidized zone is disturbed. Thus, P reactions depend on minerals present, soil reaction, and organic matter content, as well as reduction reactions. The possibility of PO_4^{3-} being reduced to form H_3P is unlikely because reduction potentials in soil are not sufficient to support this reaction [30].

Concentrations of the cations K^+, Na^+, Ca^{2+}, and Mg^{2+}, although not involved in redox reactions, also change in the solutions of waterlogged soils. During prolonged flooding, the divalent cation concentrations peak and then decrease to values similar to Fe^{2+} and Mn^{2+} concentrations in the soil solution, whereas concentrations of Na^+ and K^+ tend to decrease slowly with time, probably due to plant uptake [5].

Part of the decrease in activity of divalent cations in soil solution is attributed to ion pairing with HCO_3^- [31]. As much as 30% of the solution phase of Ca and Mg is held in the HCO_3^- form. In the case of Fe, the initial level of the ion in solution following reduction exceeded the solubility product. Iron levels in solution decreased with time [31].

The trace elements Zn and Cu are less available under reduced conditions, especially in cultivated soils [5,12]. Indications are that Zn deficiency in submerged rice soil can be partially explained by increased reduction and solubilization of Fe and Mn, which in turn have an antagonistic effect on the availability and uptake of Zn. This interpretation is supported by finding less diethylenetriaminepentaacetic-acid-(DTPA-) extractable Zn and the presence of increased CO_2 partial pressure, and consequently HCO_3^-. The HCO_3^- ion has been shown to depress the availability of Zn [32]. The usual presence of high CO_2 levels, combined with increased pH, also induces ligand formation of multivalent ions, decreasing availability of the Zn to plants.

Nitrogen undergoes numerous reactions in soil with oxidation and reduction. In wetlands, high NO_3^- concentrations may be observed in areas disturbed by cultivation or drainage, areas that served as sinks for nutrients from cultivated fields [4,33], or areas used for sewage disposal [34]. Nitrate seldom accumulates in undisturbed hydric or moist forest soils [35]. The free N that is available to plants is in the form of NH_3 or NH_4^+. The bulk of the N present is combined with organic matter. In most natural systems N turnover is slow, as indicated by wide C:N ratios in the range of 20:1 to 30:1. Under natural conditions, fairly large amounts of N can accumulate in association with organic matter [36]. Umbric forest soils in the Atlantic Coastal Plain accumulate as much as 4000 kg/ha in the surface half-meter. Histic soils can be expected to accumulate even higher levels [37]. Many of the vascular plants and microbes associated with hydric soils fix N_2. Thus, the long-term effect is for N to accumulate in hydric soils, through either fixation or sedimentation. Large accumulations may be recycled in umbric or histic soils by fires that occur from every few years up to cycles of several hundred years [38].

Carbon often accumulates as peat in hydric soils where an excess of water suppresses development of vegetation [4]. Breakdown of organic matter is slower under anaerobic conditions than it is under aerobic conditions. In aerobic soils, a three-step process occurs, each subsequent phase of the break-

down being slower than the previous phase [39]. A similar decomposition pattern was observed for lake sediments in Florida [40]. The first phase of organic matter decomposition is rapid in both aerobic and anaerobic systems; simple carbohydrates and proteins are metabolized. In the second phase, anaerobic decomposition is much slower than aerobic decomposition. In this phase, more complex organics, such as celluloses and hemicelluloses, are broken down. The difference between aerobic and anaerobic decomposition is greatest in the third phase. The metabolites in this case are materials such as lignins and lipids, which do not decompose in anaerobic peats. Moore et al. [40] found that the ratio of N and C mineralization proceeded at similar rates under both aerobic and anaerobic conditions. In lake beds, Gale and Gilmour [39] found that consolidated sediments (peat) decomposed 10 times more slowly than unconsolidated sediments at the surface of the sediment bed. They concluded that N was not a limiting nutrient in the organic decomposition process.

Anaerobic decomposition of organic matter leads to production of appreciable quantities of water-soluble organic acids, some of which can be toxic to higher plants [3,16,41]. Soil aeration results in rapid metabolism of these acids. Apparently, the production of organic acids is enhanced by the ease at which the organic matter can be metabolized under reduced conditions. When reduction potentials reach approximately −0.20 V, CH_4 is produced. Some of the CH_4 can be oxidized microbially at the soil surface, but most escapes the soil as a gas. Applications of fresh organic residues or nutrients to areas that have accumulated large amounts of organic material (peat) can accelerate CH_4 production which should be a global concern because CH_4 is a greenhouse gas. Anaerobic metabolism can also produce organic-reducing substances, such as ferulic and sinapic acids [3]. On many soils, the bulk of the reducing capacity (electron donor) is organic.

Knowledge of reduction products can be used to predict reactions and nutrient availabilities and requirements for specific sites. This capability can be important for assessing the ability of wetlands to process various chemicals in wastewater and for selecting sites for restoration. Gilmour and Gale [5] characterized hydric soils into four types on the basis of metal concentrations in solution vs. period of inundation (Fig. 2).

Type I curves represent primarily Fe and Mn in the soil solution. Concentrations in solution rise rapidly then decrease slowly to relatively stable values. The rapid increase in soluble Fe and Mn is attributed to soil reduction. The decline in metal concentration after approximately 30 d reflects a number of factors such as formation of chelates, declining CO_2 partial pressure, and possibly further reduction in the redox potential. This type of reaction is typical of the heavy soils used for grow-

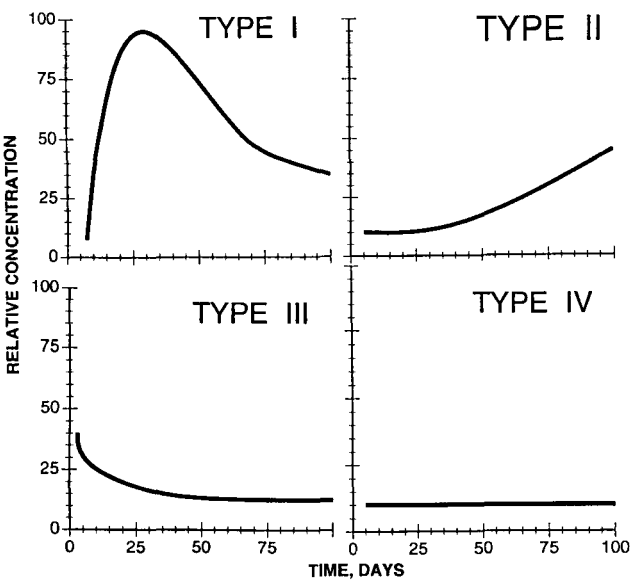

Fig. 2. Curve types for solution metal concentrations vs. time in flooded soils [5]. Reprinted with permission.

ing rice in the U.S. mid-South and river alluvial soils with high Fe content.

Type II curves are common where low temperature or lack of oxidation substrates limits the soil reduction process [5]. This type of curve occurs where amounts of Fe and Mn are limited or fertility is low. Such curves are typical of hydric soils of the flatwoods and headwater swamps of the Atlantic Coastal Plain. McKee and Hook [42] found that 40 to 60 d was required for the ratio of Fe^{3+}- to Fe^{2+}-Fe in the soil solution to reach a thermodynamic equilibrium. This ratio was associated with only a small increase in soil pH.

In type III curves, the concentration of metals in the soil solution is highest at the beginning of flooding. Under these conditions equilibrium is reached rather quickly [5]. Normally the solution phases of Cu and Zn follow this pattern. Some anion must be present to precipitate the metals. In the organic sulfaquents high in H_2S of coastal saltwater marshes, the system meets this requirement. Gilmour and Gale [5] indicate that cation exchange properties do not influence this relationship.

In type IV curves, flooding and reduction cause no appreciable change in metal concentration of soil solution. This condition is limited to totally organic soils (histisols) that have little or no mineral or clay component. It is found in freshwater organic soils that do not contain sulfides.

PLANT RESPONSES

In well-drained aerated soils, root respiration is primarily aerobic. Aerobic respiration in plants normally utilizes the tricarboxylic acid (TCA) cycle and the electron transport chain (ETC). ATP is regenerated via oxidative phosphorylation, which is coupled to the ETC. ATP is the major energy carrier in plant cell metabolism. Plants generate strongly negative electrical potentials across the plasma membrane via electrogenic pumps that are, in most cases, proton (H^+) pumps [43]. These proton pumps are membrane-bound ATPases requiring energy, usually in the form of ATP [15,44,45]. These electrical potentials provide the force necessary for the transport of both cations and anions across the plasma membrane [46]. Because nutrient uptake depends on the degree of membrane polarization, it is intimately linked to cellular respiration. Once nutrients have been transported to the xylem, their movement out of the root is primarily regulated by transpiration. Nutrients can then be selectively absorbed from the transpiration stream or adsorbed to cell walls in the xylem [47].

Toxic accumulations of some ions in mature leaf tissue are prevented by transport of mobile minerals to the phloem, where they can be recirculated through the plant [47]. However, some nutrients that are relatively immobile in the phloem accumulate in mesophyll cells. Iron is insoluble at the pH of the phloem sap, and unless it is chelated, it tends to collect in leaf tissue to toxic levels. Thus increased Fe availability on flooded sites could pose problems for some plant species.

MORPHOANATOMICAL ADAPTATIONS

In the environments where herbaceous and woody species grow, anaerobic conditions range from only a few days' exposure to saturated soil conditions to continuous exposure to flooded soils for up to two growing seasons [48]. This wide variation in soil environments appears to require a wide array of morphoanatomical and physiological adaptations among plant species. A prominent adaptation in higher plants is the ability to transport O_2 to roots. Plant species under O_2 stress have various means of avoiding root hypoxia by transporting O_2 to roots and, in some cases, the rhizosphere [49–64].

Oxygen can be transported internally and externally by simple diffusion or mass flow [65–67]. Although internal aeration systems are more common, deep-water rice possesses an external system [68]. Internal systems vary, depending on the species. In most adapted species, large air spaces, termed *aerenchyma*, have been shown to be longitudinally continuous, linking root apices with portions of the shoot above the water surface [56,69–71].

The degree and location of aerenchyma and the amount of O_2 transported to the root, as well as the O_2 demand of the root tissue, determine the ability of a root to oxidize its rhizosphere and, therefore, avoid highly reduced soil conditions [50]. Rhizosphere oxidation provides two related benefits to the submerged root system: Nutrient acquisition occurs normally, and the root system avoids exposure to toxic forms or concentrations of metals and S^{2-}. However, Conlin and Crowder [72] have suggested that rhizosphere oxidation may actually exacerbate metal toxicity problems by creating a steep concentration gradient between roots and the surrounding reduced soil.

For species lacking anatomical adaptations, changes in respiration may occur. Under aerobic conditions, O_2 is the terminal electron acceptor in the ETC. Without O_2, electrons are no longer transferred from the reduced forms of nicotinamide adenine dinucleotide (NADH) and flavin adenine dinucleotide (FADH2) through the transport chain to O_2. Oxidative phosphorylation is coupled to the ETC; therefore, further production of ATP also requires O_2. If NAD and FAD are not regenerated

via electron transport to O_2, the TCA cycle shuts down. Pyruvate accumulates until anaerobic respiration is induced, resulting in the production of lactate and then ethanol, among other possible metabolic end products [73–75]. The induction of ethanol generation appears to be pH mediated. Lactate lowers the pH of the cytoplasm, stimulating production of ethanol, which prevents cytoplasmic acidosis and further cellular damage [76]. Evidence suggests that ethanol is also transported to the shoot via the transpiration stream. Some portion of the ethanol is converted back to acetyl-CoA and enters the TCA cycle in the cells of oxidized tissues [69,76–78].

Many researchers view anaerobic respiration as a means to provide sufficient energy for survival until the development of a more porous root system or the return of a more favorable root environment [25,69,79]. The importance of anaerobic respiration in roots under hypoxic conditions varies by species. Tripepi and Mitchell [80] found that ADH activity was important to survival in river birch, where activity increased 25-fold after 6 d of hypoxia. Roberts et al. [75] concluded that activity of ADH in maize roots did not determine viability under extreme hypoxia. Waters et al. [62] have shown that ethanol production in rice occurs under both submerged and nonsubmerged conditions. Harry and Kimmerer [76] concluded that anaerobic fermentation is common in trees, regardless of soil conditions. Ernst [25] suggested that high ADH activity indicates only that the plant's metabolism is suboptimal. Further research is necessary to increase our understanding of the role of anaerobic respiration in flood tolerance.

PLANT NUTRITION

Changes in root anatomy and physiology, along with changes in soil fertility, influence nutrient uptake of plants living on wet sites. Research has shown that N, P, and K concentrations in plants are reduced by soil waterlogging, Na concentrations are increased, and other nutrients behave irregularly [16,69,81–83]. Loss of NO_3^- from the soil solution has been suggested as one cause for reduced N uptake [83]. Phosphorus is generally more available under reduced conditions, so nutrient availability alone cannot explain trends in nutrient uptake under hypoxic soil conditions.

Root hypoxia has been shown to affect nutrient uptake and translocation directly by altering plasma membrane polarization. Buwalda et al. [84] showed that root hypoxia leads to the depolarization of root cell membranes and a subsequent efflux of K from the root. Potassium flux is taken to be an indicator of the energy charge status of root system tissue, due to the coupling of cation uptake and proton extrusion with ATPase [15,85,86]. The result is that normoxic root systems are able to maintain net K^+ influx and hypoxic root systems exhibit net K^+ efflux [87].

Changes in membrane polarization may inhibit the selectivity of nutrient uptake. Excessive uptake and accumulation of Fe and, in some cases, Mn from waterlogged soil have been reported in many herbaceous and woody species [18,19,25,88–96]. Aside from direct toxic effects [25,97], Fe has been shown to be antagonistic to the uptake of other nutrients such as K, P, Ca, Mg, and Mn in rice [92,98] and P in several species [99–101]. This antagonism may be in part due to the formation of Fe plaques on roots of species that are capable of rhizosphere oxidation [99,102–106]. Iron plaque buildup enhances or reduces Zn uptake, depending on the extent of plaque formation [107]. Zinc deficiency in rice has also been related to ADH activity in the roots [108].

Ability to balance nutrient uptake and transport in a hypoxic root environment is often taken as an indicator of waterlogging tolerance. Species tolerant of waterlogging are generally capable of maintaining uptake and translocation of N, P, K, and Ca to the shoot while limiting uptake and movement of potentially toxic nutrients such as Fe and Mn [21,25,54,70,93,109–114]. Often transport from the root to the shoot is more limited than uptake, especially in the case of P [101,111,115]. Plants also adapt to hydric environments containing toxic materials by producing shallow root systems that are not in contact with reduced material lower in the soil profile.

Alteration of the native soil chemistry of a site can influence its ability to support specific plant species, as has been demonstrated by the use of P on southern pine, where P deficiency due to precipitation with Fe has been overcome [116]. In this case, the improved tree growth was attributed to elimination of a soil P deficiency, the enhancement of the plant's ability to carry on some anaerobic metabolism in the roots, and more rapid development of aerenchyma tissue [117]. Manganese toxicity in rice has been related to high Mn- and low alkali earth-cation levels.

IMPLICATIONS

Species with morphoanatomical and physiological adaptations to soil reduction are less demanding of the root environment than those that are less adapted. Less adapted species cannot survive as large a range in nutrient availability or as high a

concentration of toxic compounds in the rhizosphere. Management strategies may be used to meet the requirements of less adapted species. The season and duration of flooding can be controlled, fertilizers can be applied, and competing plant species can be eliminated. The frequency, length, and season of flooding largely determine the plant community. However, for a specific flooding regime, the nature of the soil solution and mineral content of the soil can strongly affect the fate of a species. Zinc deficiencies in rice [118] and P deficiencies in pine [13,28] are easy enough to correct. Many other species may benefit from similar treatments.

Plant communities must be carefully matched to soil and hydrological conditions to ensure success of wetland restoration or damage mitigation. The chemistry and fertility of flooded soils and the responses of individual plant species to those conditions must be understood. We know a great deal, but we have much more to learn. The knowledge is vital if wetlands are to be restored and managed for high levels of productivity, diversity, and functional value.

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