

Chapter Thirty-five

MINERAL NUTRITION OF OXYGEN-STRESSED CROPS AND ITS RELATIONSHIP TO SOME PHYSIOLOGICAL RESPONSES

R.E. Sojka and L.H. Stolzy

Historically nutritional studies of anoxic plants have simply catalogued concentration and uptake changes of treated plants, frequently on a non-partitioned whole-plant basis. Major reviews of soil aeration and flooding generally agree that N, P, and K concentrations in plants are reduced by anoxia (Kozlowski, 1984; Glinski and Stepniewski, 1985). Sodium concentration increases and other major elements either remain unaffected or react irregularly. Until recent years explanations of nutritional changes have focused chiefly on alterations in the poorly aerated soil physicochemical environment. Factors such as: increased mineral solubilization, leaching, and dilution in high water content soils, increased water film coverage of roots, altered ion diffusion, solubility changes at altered valence states, altered pH resulting from redox reactions or increased CO₂ concentrations, etc. have been used to explain nutritional responses to oxygen-limiting soil environments.

Sojka and Busscher (1986) have recently compiled an extensive plant/soil-aeration bibliography. Since the mid 1970s there has been an increase in papers relating changes in plant nutrient contents to interactions between the environment and plant physiological processes.

Farmers and many scientists (Arnon, 1937; Gilbert and Shive, 1942; Malvolta, 1954; Willhite, Grable and Rouse, 1965) have long believed that high nitrate concentrations reduce crop susceptibility to flooding. Upon flooding the falling E_h poises briefly along a series of plateaus as the soil depletes each pool of successively less-willing electron acceptors (Patrick and Mikkelson, 1971; Russell, 1976). Garcia-Novo and Crawford (1973) concluded that a specie's flood tolerance is related to effective use of nitrate as an alternative electron acceptor during anaerobiosis. Lotocki (1977) found that Scots pine (*Pinus silvestris* L.) seedlings supplied with sodium nitrate or ammonium nitrate grew better during flooding than seedlings supplied with ammonium chloride. Mixtures of ammonium and nitrate as N sources performed intermediately.

In flooded soils leaching, denitrification by micro-organisms, and volatilization occur. At least some of the decline in plant nitrogen under these conditions is probably attributable to reduced availability (Singh and Ghildyal, 1980). Few of the aeration x nutrition studies reported have been conducted in anything approaching aseptic conditions. The effects of an interacting

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microbial ecology on the root mass has not been thoroughly evaluated with respect to its effect on mineral nutrition under poorly aerated conditions. In one study (Troilidienier and von Rheinbaben, 1981) combined root/microbial respiration of wheat (*Triticum aestivum* L.) was lowest when using NO_3^- as the N source and highest with NH_4^+ as the N source. Intermediate results were obtained for mixtures. Furthermore, whereas discontinuation of K in the nutrient solutions did not affect solely nitrate-fed plants, respiration increased with $\text{NO}_3^-/\text{NH}_4^+$ mixtures and decreased with solely ammonium-fed plants when K was removed.

Reduced growth of wheat and barley (*Hordeum vulgare* L.) is more closely related to the drop in O_2 availability than to available nitrogen concentrations in flooded soils (Drew and Lynch, 1980; Trought and Drew, 1980a; Drew and Sisworo, 1977, 1979). When either NO_3^- or NH_4^+ ions were added to the aerobic soil surface or when urea was sprayed on foliar parts, chlorosis and N deficiencies associated with early stress-induced senescence of tops was prevented (Trought and Drew, 1980b). Uptake of P and K was also similarly affected by the treatments (Trought and Drew, 1980c; Drew, Jackson and Gifford, 1979).

Perhaps the most significant finding in the Letcombe experiments is the fate of plant nutrients after cessation of root uptake. Nutrients were quickly mobilized away from mature tissue to satisfy nutrient sinks in immature expanding tissue in both barley (Drew and Sisworo, 1977, 1979) and wheat (Trought and Drew, 1980b). This response was similar for N, P, and K. Earlier, Leyshon and Sheard (1974) had found that flooding effects on these nutrients were more profound in younger than mature plants. Young plants have no pool in mature tissues of easily remobilized nutrients. Also important in these studies was the rapidity of events. Root nutrient uptake halted immediately with loss of adequate root aeration, and significant nutrient redistribution was measurable in 24 to 48 h. Such time-course responses make it reasonable to consider the involvement of altered mineral-nutrition of anaerobic plants in some conspicuous physiological reactions. A good example is stomatal response to aeration.

Stomatal response is highly dynamic, responding to a variety of direct and indirect environmental stimuli. Evidence for a link between potassium nutrition and stomatal regulation has been accumulating for 80 years (McCallum, 1905; Snow, 1936). Potassium ion flux into and out of guard cells has been identified as the specific mechanism affecting guard cell turgor and hence stomatal aperture (Fujino, 1959; Fischer, 1968). It has been demonstrated that alteration of whole-plant K nutrition affects stomatal behavior (Graham and Ulrich, 1972; Wardle and Simpkins, 1979; Cooper, Blaser and Brown, 1967; Peaslee and Moss, 1966). Perhaps the most consistent nutritional response to root anoxia is reduced K uptake and plant K⁺ concentration. Hammond, Alloway and Loomis (1955) reported an approximately linear relationship between water use and K absorption from the nutrient solution by corn plants grown under varying root oxygen regimes. Moldau (1973) and Regehr, Bazzaz and Boggess (1975) reported decreased stomatal conductance to water vapor for bean leaves (*Phaseolus vulgaris* L.) under flooding equivalent to conductances seen in drought.

Moldau termed this condition 'physiological (as opposed to physical) drought.' The direct linkage of this phenomenon to oxygen removal from roots was subsequently determined for wheat (Sojka, Stolzy and Kaufmann, 1975). In a later paper Sojka and Stolzy (1980) showed that a stomatal response-threshold of $20 \times 10^{-8} \text{ g cm}^{-2} \text{ min}^{-1}$ ODR (soil oxygen diffusion rate) existed for several species studied. Plant analysis showed reduced K concentrations at the lower ODRs as well. The authors hypothesized that reduced K concentrations could interfere with normal maintenance of guard cell turgor under anoxic conditions. Decreased leaf conductance and lower K concentrations were found in a field study (Meek, Owen-Bartlett, Stolzy and Labanauskas, 1980) with cotton (*Gossypium hirsutum* L.) when water-tables were kept above 30 cm in depth.

In a recent experiment Sojka (1985) determined that the threshold ODR for soybean (*Glycine max*) is $40 \times 10^{-8} \text{ g cm}^{-2} \text{ min}^{-1}$ and that 48 h exposure to the threshold ODR was necessary to induce closure. Leaf K, Ca, and Mg were monitored in several harvests in an attempt to link K concentration changes to stomatal performance. Whole-plant tissue analyses were confounded late in the experiment and it was speculated that because significant lower leaf drop occurred, there was translocation to remaining juvenile leaves, above the position of stomatal monitoring. Although declining uptake and reduced K concentrations followed familiar trends with exposure to reduced oxygen the direct link to stomatal activity remained inconclusive. It was noted, however, that change in growth and nutrient concentrations began in the experiment at ODR thresholds less severe than that for stomatal closure, leading to the conclusion that individual physiological responses probably each have their own unique response thresholds. Peoples and Koch (1979) had earlier found that RuBPC (ribulose-1,3-bisphosphate carboxylase) synthesis, and photorespiration rates of alfalfa declined with mild K deficiency, but that stomatal closure did not occur until the deficiency became more severe. It is likely that numerous responses to reduced ODR occur in this fashion on a continuous scale of interacting primary and secondary stimuli.

Concentrations and morphological distribution of numerous hormones and their precursors including ethylene, ACC (1-amino-cyclopropane-1-carboxylic acid), CK (cytokinin), GA (gibberellins), ABA (abscisic acid), and others are drastically altered with flooding or reduced ODR (Reid and Bradford, 1984). The pervasive involvement of ethylene in flooding response, particularly in bringing about leaf epinasty coupled with the ease of its analysis led to much early speculation regarding its direct involvement in stomatal closure. Several experiments, however, would seem to indicate otherwise (Pallaghy and Raschke, 1972; Bradford, 1982, 1983; El-Beltagy and Hall, 1974; Bradford and Yang, 1981). These and other studies (Wright, 1972; Pierce and Raschke, 1980; Sivakumaran and Hall, 1978; Shaybany and Martin, 1977; Hall, Kapuya, Sivakumaran and John, 1977) have shifted interest to the role of ABA (abscisic acid) as the hormonal trigger of stomatal response during flooding. Its implication seems certain, and is consistent with the involvement of ABA in stomatal closure from drought stress (Jones and Mansfield, 1972; Hiron and Wright,

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1973; Wright, 1977). It has been shown (Jones and Mansfield, 1970) that ABA acts directly on stomatal control by impairing guard cell ability to accumulate and/or retain potassium ions (Mansfield and Jones, 1971) and by causing a transient potassium and chloride ion efflux (MacRobbie, 1981).

As stated earlier, N-deficiency, like K-deficiency, is common in leaves of poorly aerated plants. A recent series of cotton (*Gossypium hirsutum*) experiments on the interaction of N-deficiency and drought in cotton (Radin and Parker, 1979; Radin and Ackerson, 1981; Radin, 1981; Radin, Parker and Guln, 1982) produced results relevant to flood-induced stomatal closure. In these studies increased endogenous ABA content was found at high plant water potentials (ψ_p) in N-deficient plants resulting in greater stomatal sensitivity to stress. The effects of N-supply on stomata could not be explained by passive linkage to ψ_p . Stomatal closure occurred at higher ψ_p in N-deficient plants than in normal plants. A similar independence from ψ_p of stomatal response during root anoxia was reported by Sojka and Stolzy (1980). In another series of cotton experiments (Reicosky, Meyer, Schafes and Sides, 1985a; Reicosky, Smith and Meyer, 1985b; Hocking, Reicosky and Meyer, 1985) N and K levels declined in leaves following flooding. The drop in N best explained growth reductions and was also associated with increased foliage temperature and reduced photosynthesis. The latter two responses implicated stomatal closure, but that parameter was not directly observed.

Another interesting physiological response to root zone anoxia is root porosity or so-called aerenchyma tissue formation. The existence of root porosity has been known for many years (Dunn, 1921; McPherson, 1939). The topic was reviewed by Luxmoore, Sojka and Stolzy (1973). They conceived of a metabolically driven conceptual model in which high light intensity (because of its promotion of rapid growth) or oxygen shortage (relative to respiratory demand) could individually or interactively promote root air-space formation. Aerenchyma formation is widely believed an evolutionary adaptive response to low-oxygen root environments which allows increased internal O_2 diffusion to oxygen-stressed roots, thereby enabling continued aerobic respiration. Even in the new mass flow theory of O_2 to submerged rice (*Oryza sativa*) roots (Raskin and Kende, 1983, 1985), formation of high porosity favors survival due to the reduction in pathway resistance.

Interplay of mineral nutrition as a root air space formation factor has gone largely uninvestigated. A few recent reports, however, suggest that mineral nutrition may be an important consideration. Konings and Verschuren (1980) reported a relationship between a decline in nutrient solution N (as NO_3^- or as NH_4^+) and increased root air-space development. They explained the promotion of root porosity observed by Luxmoore et al. (1972) during high light intensity periods or elevated temperature on the basis of a NO_3^- shortage in the roots during a period of high assimilatory demand. Hardcastle and Schutte (1983) found that if maize (*Zea mays*) roots were grown either in anaerobic solutions or in solutions deficient in nitrate and phosphate that root porosity increased. Furthermore, they observed that air-space formation in

nutrient-deficient solutions was more severe when the solutions were anaerobic.

The issue appears to be more complicated, however, with ethylene playing a role in maize root aerenchyma formation as well (Drew, Sisworo and Sakes, 1979; Drew, Jackson, Gifford and Campbell, 1981; Konings, 1982). Nutrient levels were never limiting in these studies, and thus the influence of N metabolism in mediating the ethylene response remains undefined. Jackson, Fenning and Jenkins (1985) found no ethylene influence on aerenchyma formation in rice and that its development proceeded regardless of O_2 status. Others have observed greater root porosity development in rice at low O_2 partial pressure (Armstrong, 1971; Das and Jat, 1977). Konings and de Wolf (1984) found that other growth-regulating substances affected aerenchyma formation on non-aerated or NO_3^- -starved roots as well, but that their action did not occur through mediation of ethylene.

A particularly interesting aspect of the work by Drew et al. (1979) was that while very low O_2 levels stimulated ethylene production and root aerenchyma formation, both were halted by absolute removal of O_2 . Phosphorus has not been studied separately in relation to aerenchyma formation but Jackson, Drew and Gifford (1981) showed that ethylene exposure contributed to reduced phosphorus uptake in roots similar to flooding, but without an effect on N or K. It seems that while ethylene may be active in root porosity induction its production and activation may require the gradual reduction of O_2 , possibly allowing a precursor such as ACC to be produced. Aeration-induced nutritional deficiency may be involved as an added stress signal inducing ethylene production. In the transition environment between drained and inundated soil these factors may come together synergistically. Interestingly, it has been reported that ABA, which is linked to stomatal closure of flooded plants, is a naturally occurring inhibitor of aerenchyma formation (Konings and de Wolf, 1984).

Another root response affected by flooding is geotropism. Root penetration decreases into waterlogged or otherwise poorly aerated horizons and roots may follow shallower angles or even grow above the anoxic zone at the interface of the adequately aerated surface soil (Ycas and Zobel, 1983; Wiersum, 1979; Papenhuijzen, 1979; Nazrul Islam, Saha and Khan, 1980; Jackson, 1985). A report by Bejaoui (1980) indicated an interaction of sodium ion and oxygen uptake in this phenomenon. In his work 50 mM NaCl in addition to inhibiting growth and oxygen uptake by roots, increased their geotropic sensitivity with the effect more pronounced in lateral roots. Sodium concentration is commonly observed to increase in oxygen-stressed plants (Labanauskas et al., 1986, 1971, 1972, 1975; Leggett and Stolzy, 1961; Passoa da Costa and Smucker, 1981; Letey et al., 1961, 1962, 1965; Drew and Dikumwin, 1985; Drew and L uchli, 1985). Anaerobic Na uptake is a metabolically coupled process (Leggett and Stolzy, 1961). In their work, Na uptake by roots of anaerobic plants decreased with time indicating that some process was 'attenuating'. They interpreted this to show that Na uptake was metabolically driven but several steps removed from the respiratory process. In an anoxic pretreatment, anaerobiosis per se did not activate Na

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uptake in shoots, instead it increased the Na uptake rate on returning to aerobic conditions. Root and shoot uptake appeared to involve separate processes. The effects of low soil O₂ and root Na uptake may act to counter one another. The geotropic stimulus of Na may dampen the apparently hormonally induced lateral stimulus of root growth or may reinitiate geotropic response when the soil profile drains.

Various attempts have been made to nutritionally ameliorate anaerobic (usually flooded) soils (Karlen, Sojka and Robbins, 1983; Ponnampuruma, Yuan and Nhung, 1965; Trought and Drew, 1980, 1981; Drew et al., 1979; McKee, Hook, DeBell and Askew, 1984; Bryce, Fochi and Stolzy, 1982; Herr and Jarrell, 1980; Hodgson, 1982; Magunda, Callebaut, DeBoot and Gabriels, 1984). These efforts have usually been aimed at N involvement in the anaerobic metabolism (as discussed earlier), at combatting specific nutrient deficiencies in flooded soils, or at providing so-called 'oxygen fertilizers' to ameliorate directly the soil redox status. In both of the two latter approaches the success has depended somewhat on flooding duration at time of treatment, method, and amount of application and plant growth stage. Oxygen fertilization, while promising in some instances, is expensive and may not be practical on a field scale for all but high value crops or ornamentals or in glasshouse operations. The effectiveness of all the approaches is very much affected by the severity of the anaerobic regime being combatted.

CONCLUSION

This review has not been all-inclusive, but illustrates application of concepts of mineral nutrition to the understanding and improved management of crop growth under anaerobic conditions.

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