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hydrophyte at anoxia and after glucose feeding. Protoplasma, 91, 243-56
Vartapetian, B.B., Andreeva, I.N. and Nutridinov, N. (1978) Plant cells under oxygen stress. In D.D. Hook and R.M.M. Crawford (eds), Plant life in anaerobic environments, Ann Arbor Press, Ann Arbor, MI, pp. 13-88
Vartapetian, B.B., Zakhmylova, N.A. and Generozova, I.P. (1985) Ultrastructure of wheat coleoptile mitochondria at short-term anoxia and post anoxia. Plant, Cell Environ., 8, 65-7
Vester, G. and Crawford, R.M.M. (1978) Verschiedene provenienzen von Pinus contorta Louden und Uberflutungsstre B: Klassifikation auf grund morphologischer und metabolischer Kriterien. Flora, 167, 433-44
Wainwright, S.J. (1984) Adaptations of plants to flooding with salt water. In T.T. Kozlowski (ed.), Flooding and plant growth, Academic Press, New York, pp. 295-343
Webb, T. and Armstrong, W. (1983) The effects of anoxia and carbohydrates on the growth and viability of rice, pea and pumpkin roots. J. Exp. Bot., 34, 579-603
Wiegert, R.G., Chalmers, A.G. and Randerson, P.F. (1983) Productivity gradients in salt marshes: the response of Spartina alterniflora to experimentally manipulated soil water movement. Oikos, 41, 1-6
Wignarajah, K., Greenway, H. and John, C.D. (1976) Effect of waterlogging on growth and activity of alcohol dehydrogenase in barley and rice. New Phytol., 77, 585-92
Wu, L. (1981) The potential for evolution of salinity tolerance in Agrostis stolonifera L. and Agrostis tenuis Sibth. New Phytol., 89, 471-86
Zaerr, J.B. (1983) Short-term flooding and net photosynthesis in seedlings of three conifers. Forest Sci., 29, 71-8
Zemlianukhin, A.A. and Ivanov, B.F. (1978) Metabolism of organic acids of plants in the conditions of hypoxia. In D.D. Hook and R.M.M. Crawford (eds), Plant life in anaerobic environments, Ann Arbor Press, Ann Arbor, MI, pp. 203-68

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 CO_2 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

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 (Trolldenier 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 NO_3^-/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 x 10^{-8} g cm^{-2} 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 x 10^{-8} g cm^{-2} 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-aminocyclopropane-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, Sirakumaran 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

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 Guinn, 1982) produced results relevant to flood-induced stomatal closure. In these studies increased endogenous ABA content was found at high plant water potentials (ψ_ρ) 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_ρ. Stomatal closure occurred at higher ψ_ρ in N-deficient plants than in normal plants. A similar independence from ψ_ρ of stomatal response during root anoxia was reported by Sojka and Stolzy (1980). In another series of cotton experiments (Reicosky, Meyer, Schasfes 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 (1972). 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 (Yeas 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., 1966, 1971, 1972, 1975; Leggett and Stolzy, 1961; Pessoa da Costa and Smucker, 1981; Letey et al., 1961, 1962, 1965; Drew and Dikumwin, 1985; Drew and Läuchli, 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

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 O_2 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; Ponnamperuma, Yuan and Nhung, 1965; Trought and Drew, 1980, 1981; Drew et al., 1979; McKee, Hook, DeBell and Askew, 1984; Bryce, Focht 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 anoxic 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.

REFERENCES

Armstrong, W. (1971) Radial oxygen losses from intact rice roots as affected by distances from the apex, respiration and waterlogging. Physiol. Plant., 25, 192-7

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

Bejaoui, M. (1980) Effects du NaCl sur l'elongation, la georeaction et l'absorption d'oxygene de segments apicaux de racines de soja (Glycine max (L.) Merr.). Physiol. Veg., 18, 737-47

Bradford, K.J. (1982) Regulation of shoot responses to root stress by ethylene, abscisic acid, and cytokinin. In P.F. Warring Plant growth substances, Academic Press, London, pp. 599-608

Bradford, K.J. (1983) Involvement of plant growth substances in the alteration of leaf gas exchange of flooded tomato plants. Plant Physiol., 73, 480-3

Bradford, K.J. and Yang, S.F. (1981) Physiological responses of plants to waterlogging. HortScience, 16, 25-30

Bryce, J.H., Focht, D.D. and Stolzy, L.H. (1982) Soil aeration and plant growth response to urea peroxide fertilization. Soil Sci., 134, 111-16

Cooper, R.B., Blaser, R.E. and Brown, R.H. (1967) Potassium nutrition effects on net photosynthesis and morphology of alfalfa. Soil Sci. Soc. Am. Proc., 31, 231-5

Das, D.K. and Jat, R.L. (1977) Influence of three soil-water regimes on root porosity and growth of four rice varieties. Agron. J., 69, 197-200

Drew, M.C. and Dikumwin, E. (1985) Sodium exclusion from the shoot by roots of Zea mays (cv. LG11) and its breakdown with oxygen deficiency. J. Exp. Bot., 36, 55-62

Drew, M.C., Jackson, M.B. and Gifford, S. (1979) Ethylene-promoted adventitious rooting and development of cortical air spaces (aerenchyma) in roots may be adaptive responses to flooding i: Zea mays L. Planta, 147, 83-8

Drew, M.C., Jackson, M.B., Gifford, S.C. and Campbell, R. (1981) Inhibition by silver ions of gas space (aerenchyma) formation in adventitious roots of Zea mays L. subjected to exogenous ethylene or to oxygen deficiency. Planta, 153, 217-24

Drew, M.C. and Läuchli, A. (1985) Oxygen-dependent exclusion of sodium ions from shoots by roots of Zea mays (cv. Pioneer 3906) in relation to salinity damage. Plant Physiol., 79, 171-6.L

Drew, M.C. and Lynch, J.M. (1980) Soil anaerobiosis, microorganisms, and root function. Ann. Rev. Phytopathol., 18, 37-66

Drew, M.C. and Sisworo, E.J. (1977) Early effects of flooding on nitrogen deficiency and leaf chlorsis in barley. New Phytol., 79, 567-71

Drew, M.C. and Sisworo, E.J. (1979) The development of waterlogging damage in young barley plants in relation to plant nutrient status and changes in soil properties. New Phytol., 82, 301-14

Drew, M.C., Sisworo, E.J. and Saker, L.R. (1979) Alleviation of waterlogging damage to young barley plants by application of nitrate and a synthetic cytokinin, and comparison between the effects of waterlogging, nitrogen deficiency and root excision. New Phytol., 82, 315-29

Dunn, G.A. (1921) Note on the histology of grain roots. Am. J. Bot., 8, 207-11

El-Beltagy, A.S. and Hall, M.A. (1974) Effect of water stress upon endogenous ethylene levels in Vicia faba. New Phytol., 73, 47-60

Fischer, R.A. (1968) Stomatal opening: role of potassium ion uptake by guard cells. Science, 168, 784-5

Fujino, M. (1959) Stomatal movement and active migration of potassium (Japanese). Kagaku, 29, 600-61

Garcia-Novo, F. and Crawford, R.M.M. (1973) Soil aeration, nitrate reduction and flooding tolerance in higher plants. New Phytol., 72, 1031-9

Gilbert, S.G. and Shive, J.W. (1942) The significance of oxygen in nutrient substrates for plants: The oxygen requirement. Soil Sci., 53, 143-52

Glinski, J. and Stepniewski, W. (1985) Soil aeration and its role

for plants. CRC Press, Boca Raton, 229 pp.
Graham, R.D. and Ulrich, A. (1972) Potassium deficiency-induced changes in stomatal behavior, leaf water potentials, and root system permeability in Beta vulgaris L. Plant Physiol., 49, 105-9
Hall, M.A., Kapuya, J.A., Sivakumaran, S. and John A. (1977) The role of ethylene in the responses of plants to stress. Pest. Sci., 8, 217-23
Hammond, L.C., Alloway, W.H. and Loomis, W.E. (1955) Effects of oxygen and carbon dioxide levels upon absorption of potassium by plants. Plant Physiol., 30, 155-61
Hardcastle, J. and Schutte, K.H. (1983) Aspects of an experimental study on root aerenchyma development and the ecological implications thereof. Bothalia, 14, 791-4
Herr, E.M. and Jarell, W.M. (1980) Response of chrysanthemum to urea peroxide. HortScience, 15, 501-2
Hiron, R.W.P. and Wright, S.T.C. (1973) The role of endogenous abscisic acid in the response of plants to stress. J. Exp. Bot., 24, 769-81
Hocking, P.J., Reicosky, D.C. and Meyer, W.S. (1985) Nitrogen status of cotton subjected to two short term periods of waterlogging of varying severity using a sloping plot water-table facility. Plant Soil, 87, 375-91
Hodgson, A.S. (1982) The effects of duration, timing and chemical amelioration of short-term waterlogging during furrow irrigation of cotton in a cracking grey clay. Aust. J. Agric. Res., 33, 1019-28
Jackson, M.B. (1985) Ethylene and responses of plants to soil waterlogging and submergence. Ann. Rev. Plant Physiol., 36, 145-74
Jackson, M.B., Drew, M.C. and Gifford, S.C. (1981) Effects of applying ethylene to the root system of Zea mays on growth and nutrient concentration in relation to flooding tolerance. Physiol. Plant., 52, 23-8
Jackson, M.B., Fenning, T.M. and Jenkins, W. (1985) Aerenchyma (gas-space) formation in adventitious roots of rice (Oryza sativa L.) is not controlled by ethylene or small partial pressures of oxygen. J. Exp. Bot., 36, 1566-72
Jones, R.J. and Mansfield, T.A. (1970) Suppression of stomatal opening in leaves treated with abscisic acid. J. Exp. Bot., 21, 714-19
Jones, R.J. and Mansfield, T.A. (1972) Effects of abscisic acid and its esters on stomatal aperture and the transpiration ratio. Physiol. Plant., 26, 321-7
Karlen, D.L., Sojka, R.E. and Robbins, M.L. (1983) Influence of excess soil-water and N-rates on leaf diffusive resistance and storage quality of tomato fruit. Commun. Soil Sci. Plant Anal., 14, 699-708
Konings, H. (1982) Ethylene-promoted formation of aerenchyma in seedling roots of Zea mays L. under aerated and non-aerated conditions. Physiol. Plant., 54, 119-24
Konings, H. and de Wolf, A. (1984) Promotion and inhibition by plant growth regulators of aerenchyma formation in seedling roots of Zea mays. Physiol. Plant., 60, 309-14
Konings, H. and Verschuren, G. (1980) Formation of aerenchyma in roots of Zea mays in aerated solutions, and its relation to nutrient supply. Physiol. Plant., 49, 265-70
Kozlowski, T.T. (ed.) (1984) Flooding and plant growth. Academic Press, New York, 356 pp.
Labanauskas, C.K., Letey, J., Stolzy, L.H. and Valoras, M. (1966) Effects of soil-oxygen and irrigation on the accumulation of macro-and micronutrients in citrus seedlings (Citrus sinensis Var. Osbeck). Soil Sci., 101, 378-84
Labanauskas, C.K., Stolzy, L.H. and Handy, M.F. (1972) Concentrations and total amounts of nutrients in citrus seedlings (Citrus sinensis Var. Osbeck) and in soil as influenced by differential soil oxygen treatments. Soil Sci. Soc. Am. Proc. 36, 457-64
Labanauskas, C.K., Stolzy, L.H., Klotz, L.J. and de Wolf, T.A. (1971) Soil oxygen diffusion rates and mineral accumulations in citrus seedlings (Citrus sinensis Var. Bessie). Soil Sci., 111, 386-92
Labanauskas, C.K., Stolzy, L.H. and Luxmoore, R.J. (1975) Soil temperature and soil aeration effects on concentrations and total amounts of nutrients in 'Yecora' wheat grain. Soil Sci., 120, 450-4
Leggett, J.E. and Stolzy, L.H. (1961) Anaerobiosis and sodium accumulation. Nature, 192, 991-2
Letey, J., Stolzy, L.H., Blank, G.B. and Lunt, O.R. (1961) Effect of temperature on oxygen-diffusion rates and subsequent shoot growth, root growth, and mineral content of two plant species. Soil Sci., 92, 314-21
Letey, J., Stolzy, L.H. and Valoras, N. (1965) Relationships between oxygen diffusion rate and corn growth. Agron. J., 57, 91-2
Letey, J., Stolzy, L.H., Valoras, N. and Szuszkiewicz, T.E. (1962) Influence of soil oxygen on growth and mineral concentration of barley. Agron. J., 54, 538-40
Leyshon, A.J. and Sheard, R.W. (1974) Influence of short-term flooding on the growth and plant nutrient composition of barley. Can. J. Soil Sci., 54, 463-73
Lotocki, A. (1977) Effect of root aeration and form of nitrogen on photosynthetic productivity of Scots pine (Pinus silvestris L.). Acta Soc. Bot. Polon., 46, 303-16
Luxmoore, R.J., Sojka, R.E. and Stolzy, L.H. (1972) Root porosity and growth responses of wheat to aeration and light intensity. Soil Sci., 113, 354-7
McCallum, A.B. (1905) On the distribution of potassium in animal and vegetable cells. J. Physiol. (London), 32, 95-118
McKee, W.H., Jr, Hook, D.D., DeBell, D.S. and Askew, J.L. (1984) Growth and nutrient status of loblolly pine seedlings in relation to flooding and phosphorus. Soil Sci. Soc. Am. J., 48, 1438-42
McPherson, D.C. (1939) Cortical air spaces in the roots of Zea mays L. New Phytol., 38, 190-202
MacRobbie, E.A.C. (1981) Effects of ABA in isolated guard cells of Commelina communis L. J. Exp. Bot., 32, 563-72
Magunda, M.K., Callebaut, F., DeBoot, M. and Gabriels, D. (1984)

, Role of calcium peroxide as a soil conditioner and oxygen fertilizer. Trop. Agric., (Trinidad), 61, 250-2
Malovolta, E. (1954) Studies on the nitrogenous nutrition of rice. Plant Physiol., 29, 98-9
Mansfield, T.A. and Jones, R.J. (1971) Effects of abscisic acid on potassium uptake and starch content of stomatal guard cells. Planta, 101, 147-58
Meek, B.D., Owen-Bartlett, E.C., Stolzy, L.H. and Labanauskas, C.K. (1980) Cotton yield and nutrient uptake in relation to water table depth. Soil Sci. Soc. Am. J., 44, 301-5
Moldau, H. (1973) Effects of various water regimes on stomatal and mesophyll conductances of bean leaves. Photosynthetica, 7, 1-7
Nazrul Islam, A.K.M., Saha, U.S. and Khan, M.R. (1980) Some aspects of the physiology and ecology of soybean under waterlogged and non-waterlogged condition. Bangladesh J. Bot., 9, 54-9
Pallaghy, C.K. and Raschke, K. (1972) No stomatal response to ethylene. Plant Physiol., 49, 275-6
Papenhuijzen, C. (1979) A comparison of the morphological development of aerated and non-aerated primary root systems of Phaseolus vulgaris L. Acta Bot. Neerl., 28, 281-7
Patrick, W.H. and Mikkelson, D.S. (1971) Plant nutrient behavior in flooded soil. In R.A. Olson, T.J. Army, J.J. Hanway and V.J. Kilmer (eds), Fertilizer technology and use, Soil Science Society of America, Madison, WI, pp. 187-215
Peaslee, D.E. and Moss, D.N. (1966) Stomatal conductivities in K-deficient leaves of maize (Zea mays L.). Crop Sci., 8, 427-30
Peoples, T.R. and Koch, D.W. (1979) Role of potassium in carbon dioxide assimilation in Medicago sativa L. Plant Physiol., 63, 878-81
Pessoa de Costa, G.T. and Smucker, A.J.M. (1981) Interactions of oxygen-nitrogen-salinity stresses on plant growth and mineral content of sunflower (Helianthus annuus L.) in sand culture. J. Plant Nutr., 3, 887-903
Pierce, M. and Raschke, K. (1980) Correlation between loss of turgor and accumulation of abscisic acid in detached leaves. Planta, 148, 174-82
Ponnamperuma, F.N., Yuan, W.L. and Nhung, M.T.M. (1965) Manganese dioxide as a remedy for a physiological disease of rice associated with reduction of the soil. Nature, 207, 1103-4
Radin, J.W. (1981) Water relations of cotton plants under nitrogen deficiency. IV. Leaf senescence during drought and in its relation to stomatal closure. Physiol. Plant., 51, 145-9
Radin, J.W. and Ackerson, R.C. (1981) Water relations of cotton plants under nitrogen deficiency. III. Stomatal conductance, photosynthesis, and abscisic acid accumulation during drought. Plant Physiol., 67, 115-19
Radin, J.W. and Parker, L.L. (1979) Water relations of cotton plants under nitrogen deficiency. II. Environmental interactions on stomata. Plant Physiol., 64, 499-501
Radin, J.W., Parker, L.L. and Guinn, G. (1982) Water relations of cotton plants under nitrogen deficiency. V. Environmental control of abscisic acid accumulation and stomatal sensitivity to abscisic acid. Plant Physiol., 70, 1066-70
Raskin, I. and Kende, H. (1983) How does deep water rice solve i aeration problem? Plant Physiol., 72, 447-54
Raskin, I. and Kende, H. (1985) Mechanism of aeration in rice. Science, 228, 327-9
Regehr, D.L., Bazzaz, F.A. and Boggess, W.R. (1975) Photosynthes transpiration, and leaf conductance of Populus deltoides ir relation to flooding and drought. Photosynthetica, 9, 52-61
Reicosky, D.C., Meyer, W.S., Schaefer, N.L. and Sides, R.D. (198 Cotton response to short-term waterlogging imposed with a water-table gradient facility. Agric. Water Mgt., 10, 127-4
Reicosky, D.C., Smith R.C.G. and Meyer, W.S. (1985b) Foliage temperature as a means of detecting stress of cotton subjec to a short-term water-table gradient. Agric. For. Met., 35, 193-203
Reid, D.M. and Bradford, K.J. (1984) Effects of flooding on horm relations. In T.T. Kozlowski (ed.), Flooding and plant grow Academic Press, Orlando, pp. 195-219
Russell, E.W. (1976) The chemistry of waterlogged soils. In E.W. Russell (ed.) Soil conditions and plant growth, Longmans, N York, p. 849
Shaybany, B. and Martin, G.C. (1977) Abscisic acid identificatic and its quantitation in leaves of Juglans seedlings during waterlogging. J. Am. Soc. Hortic. Sci., 102, 300-2
Singh, R. and Ghildyal, B.P. (1980) Soil submergence effects on nutrient uptake, growth and yield of five corn cultivars. Agron. J., 72, 737-41
Sivakumaran, S. and Hall, M.A. (1978) Effects of age and water stress on endogenous levels of plant growth regulators in Euphorbia lathyrus L. J. Exp. Bot., 29, 195-205
Snow, A.G., Jr (1936) Transpiration as modified by potassium. Pl Physiol., 11, 583-94
Sojka, R.E. (1985) Soil-oxygen effects on two determinate soybea isolines. Soil Sci., 140, 333-43
Sojka, R.E. and Busscher, W.J. (1986) A computer-based plant/soi aeration bibliography. Proceedings of Poster Papers. In D.I Hook et al., Ecology and management of wetlands Vol II management, use and value of of wetlands, Croom Helm Ltd., Kent, UK, pp. 284-9
Sojka, R.E. and Stolzy, L.H. (1980) Soil-oxygen effects on stoma response. Soil Sci., 130, 350-8
Sojka, R.E., Stolzy, L.H. and Kaufmann, M.R. (1975) Wheat growth related to rhizosphere temperature and oxygen levels. Agron J., 67, 591-6
Trolldenier, G. and von Rheinbaben (1981) Root respiration and bacterial population of roots. I: Effects of nitrogen sourc potassium nutrition and aeration of roots. Z. Pflanzenernae Bodink., 144, 366-77
Trought, M.C.T. and Drew, M.C. (1980a) The development of waterlogging damage in wheat seedlings (Triticum aestivum L.) I. Shoot and root growth in relation to changes in the concentrations of dissolved gases and solutes in the soil solutio Plant Soil, 54, 77-94
Trought, M.C.T. and Drew, M.C. (1980b) The development of waterlogging damage in wheat seedlings (Triticum aestivum L.) II

Accumulation and redistribution of nutrients by the shoot. Plant Soil, 56, 187-99

Trought, M.C.T. and Drew, M.C. (1980c) The development of waterlogging damage in wheat plants in anaerobic solution culture. J. Exp. Bot., 31, 1573-85

Trought, M.C.T. and Drew, M.C. (1981) Alleviation of injury to young wheat plants in anaerobic solution cultures in relation to the supply of nitrate and other inorganic nutrients. J. Exp. Bot., 32, 509-22

Wardle, K. and Simpkins, I. (1979) Stomatal responses of Phaseolus vulgaris L. seedlings to potassium chloride in the nutrient solution. J. Exp. Bot., 30, 1195-200

Wiersum, L.K. (1979) A comparison of the behavior of some root systems under restricted aeration. Neth. J. Agric. Sci., 27, 92-8

Willhite, F.M., Grable, A.R. and Rouse, H.K. (1965) Interaction of nitrogen and soil moisture on the production and persistence of timothy in lysimeters. Agron. J., 57, 479-81

Wright, S.T.C. (1977) The relationship between leaf water potential (leaf) and the levels of abscisic acid and ethylene in excised wheat leaves. Planta, 134, 183-9

Wright, S.T.C. (1972) Physiological and biochemical responses to wilting and stress conditions. pp. 349-361. In A.R. Rees, K.E. Cockshull, D.W. Hand and R.D. Hurd (eds), Crop processes in controlled environments, Academic Press, London

Yčas, J.W. and Zobel, R.W. (1983) The response of maize radicle orientation to soil solution and soil atmosphere. Plant Soil, 70, 27-35

Chapter Thirty-six

RESPONSES OF WOODY SEEDLINGS TO ELEVAT FLOOD WATER TEMPERATURES

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Multiple stresses acting simultaneously may aff same, or less than each would individually. Wit of environmental stresses created by man's ac the effects of a single stress is exceptionally stress (e.g. flooding, high temperature, chem usually affects many aspects of the physical er ing both positive and negative results. Deterr as well as the interactions of several stresses to achieve a predictive capacity for multiple s individual effects of flooding and high substr be briefly reviewed, after which their comb growth, morphology and physiology of woody discussed.

FLOOD STRESS

The terms flooded, saturated and waterlogged ences in the amount of standing water present, soil environments. Changes that occur follow reduced O_2 and increased CO_2 content of th 1975). The rapidity of these changes depends c (root and microbial) in the soil and on diffusio the water column and the soil. Diffusion is varies with water depth, temperature, and oxygen is limited, Fe and Mn are converted forms. Biota may modify this anoxic soil condi term but their impact is small in the short-term flooding, plant roots are subjected to anoxic c flooding affects the whole plant, not simply t rectly exposed to the stress. Indirect effects or of the plant are expressed through changes i hormone production and other root-controlled pr

Stresses such as flooding change the abiot both spatial and temporal scales. Plants respon the stress, but the response depends on whe capable of surviving short, moderate, or long Some species are evolutionarily adapted to w