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STOMATAL CLOSURE IN OXYGEN-STRESSED PLANTS

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Stomatal closure of plants in flooded soil, as determined by leaf gas exchange, has been recognized since 1973, and for simple hypoxia since 1975. At least 58 species have been shown to close stomata with hypoxic or flooded conditions. Various factors interact to affect the relationship between rhizosphere oxygen availability, as measured by soil oxygen diffusion rate (ODR), and degree of stomatal closure. These factors include root temperature, species, plant growth stage, plant mineral nutrition, and duration and nature of hypoxia. Soil water content, bulk density, and temperature also influence ODR. Abscisic acid accumulation in leaves appears to induce stomatal closure, as a stress response to root hypoxia, through its effect on potassium ion regulation of guard cell turgor. Stomatal closure generally persists well beyond actual soil hypoxia. Photosynthesis is reduced by root hypoxia, both by reduction of leaf gas exchange and by a lowering of the photosynthetic rate at a given leaf gas exchange rate. This phenomenon deserves greater attention in evaluating and modelling of crop response to soil hypoxia and as a sensitive indicator of severity of soil hypoxic stress.

Many deleterious effects of waterlogging on plants have been recognized for centuries (Clements 1921). As early as 1853 (Boussignault and Lewy 1853) soil oxygen's specific role in maintaining plant vigor was recognized. By the 1950's, some plant physiological flooding responses were known to resemble drought responses (Kramer and Jackson 1954). A commonly noted expression of this syndrome was the rapid wilting of susceptible crops such as tobacco (*Nicotiana tabacum*) and tomato (*Lycopersicon esculentum*).

As instrumentation has become available to monitor stomatal gas exchange, it has become apparent that stomatal closure is an important component of whole-plant stress response to root zone oxygen deprivation. This paper traces the development of information on root oxygen-related stomatal response. Several suggestions are offered for application of current knowledge and for further research.

RECOGNITION OF THE PHENOMENON

Childers and White (1942) documented reduced transpiration and photosynthesis within 2 to 7 days after flooding of apple trees (*Malus domestica*). Slight elevation of transpiration and photosynthesis immediately upon inundation reflected relief of minor water stress. Flooding caused extensive root necrosis and reduced leaf expansion, but percent of open plus partially open stomata and leaf temperature were unaffected. These results resemble most findings of related studies to the present day. Current understanding of leaf conductance and of technical limitations of thermocouple thermometry, however, challenges their original interpretation that stomata and leaf temperature were unaffected.

Increased leaf diffusive resistance (the reciprocal of leaf conductance) with flooding was first measured by Moldau (1973) for bean plants (*Phaseolus vulgaris*). A similar observation was reported in 1975 by Regehr et al. for *Populus deltoides*. These first measurements of increased leaf diffusive resistance (R_L) confirmed that flooding impairs normal plant control of leaf gas exchange and regulation of water and solute transport. They also provided a credible explanation for earlier observations of reduced leaf damage by airborne oxidants when exposure occurred during flooding (Stolzy et al. 1961; Dugger and Ting 1970).

Various causative mechanisms of plant flooding response had been implicated, including obstruction of xylem elements by disease organisms, increased root membrane resistance to water, and plant nutritional and hormonal imbalances caused by flooding (Kramer and Jackson 1954; Bradford 1982; Stolzy and Sojka 1984). It was generally assumed that exclusion of oxygen from the rhizosphere was involved in the predisposition of plants to this syndrome. Indeed a substantial body of work has used con-

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TABLE 1

Species for which R_L has been shown to increase in response to root-zone flooding or hypoxia

Species	Stimulus	Citation
Acer rubrum	soil O_2 + CH_4	8
Acer saccharum	soil O_2 + CH_4	8
Actinidia chinensis	flood	95
	anoxic soln.	108
Apios americana	flood	62
Avicennia marina	flood	64
Betula papyrifera	flood	68
Betula nigra	flood	68
Betula platyphylla	flood	122
Bruguiera gymnorrhiza	flood + salt	65
	flood	64
Citrus aurantium	flood	118, 123
Citrus jambhiri	flood	118, 123
Citrus sinensis	flood	123
Capiscum annuum	flood	84
Carya illinoensis	Soil O_2	109
	flood	107, 125
Cydonia oblonga	anoxic soln.	7
	flood	6
Eucalyptus camaldulensis	flood	12, 79
Eucalyptus globulus	flood	12, 79
Eucalyptus obliqua	flood	12
Fraxinus pennsylvanica	flood	49, 79, 99, 120
Glycine max	flood	70, 71
	Soil O_2	110
Gmelina arborea	flood	73, 74
Gossypium barbadense	Soil O_2	112
Gossypium hirsutum	flood	58
	Soil O_2	112
Helianthus annuus	anoxic soln.	31
	flood	34, 72
	anoxic soln. + salt	51, 52
	Soil O_2 + heat	112, 113
Hydrangea macrophylla	flood	102
Liquidambar styraciflua	flood	81
Lycopersicon esculentum	flood	15, 16, 17, 18, 46, 53, 86
Malus domestica	flood	6, 69
Melaleuca quinquenervia	flood	100
Nauclea diderrichii	flood	74
Nyssa aquatica	flood + heat	28
Phaseolus vulgaris	flood	59, 96
	anoxic soln.	65, 96, 97, 66
Picea glauca	flood + heat	33
Picea mariana	flood + heat	33
Pisum sativum	flood	42, 43, 132
Poa pratensis	compaction + irr.	3
Populus deltoides	flood	79, 91
P. trichocarpa × deltoides	anoxic soln.	65, 105, 106
Prunus persica	anoxic soln.	7
	flood	6, 10
Pyrus betulaefolia	anoxic soln.	5, 7
	flood	6
Pyrus calleryana	anoxic soln.	5, 7
	flood	6

TABLE 1. *Continued*

Species	Stimulus	Citation
Pyrus communis	anoxic soln.	5, 7
	flood	6
Pyrus pyrifolia	flood	6
Pyrus ussuriensis	flood	6
Quercus falcata	flood	80
Quercus macrocarpa	flood	119
Quercus rubra	flood	79
Rhizophora mucronata	flood	64
Salix discolor	anoxic soln.	7
	flood	6
Salix nigra	flood	79
Simmondsia chinensis	Soil O_2 + heat	112, 113
Sorghum bicolor	flood	72
Tectona grandis	flood	74
Theobroma cacao	flood	101
Triticum aestivum	Soil O_2 + heat	111, 112, 113
Ulmus americana	flood	67, 79
Vaccinium ashei	flood	25
Vaccinium corymbosum	flood	1, 24
Zea mays	anoxic soln.	96, 126

trolled soil atmospheres to elicit various physiological, nutritional, and pathological responses seen with flooding (Stolzy and Sojka 1984). Sojka et al. (1975) measured increased R_L when soil oxygen was excluded from roots of wheat (*Triticum aestivum*) grown at optimal water and nutritional levels. This finding confirmed that during flooding, the physiological and metabolic processes ultimately resulting in stomatal closure were linked to inadequate oxygen diffusion to living roots.

Increased R_L associated with poor soil aeration has been documented for at least 58 species (Table 1). Though beyond the scope of this paper, it is important to note that many papers that did not monitor R_L per se have instead reported such closely related variables as apparent photosynthesis, transpiration, water use, and leaf CO_2 absorption in relation to rhizosphere flooding and hypoxia (e.g., Phung and Knipling 1976; Coutts 1981; Pezeshki et al. 1989). Table 1 reveals that most studies utilized flooding of roots in soil as the method of oxygen exclusion. Many flooding studies documented the soil oxygen diffusion rate (ODR) or redox potential (E_h) of the root zone.

Flooding is the most common field soil hypoxic syndrome, but its effect on plant oxygen relationships is confounded by interactions of non-oxygen factors in the flooded environment (e.g., by nutrient losses, diseases, nematodes, trace-gas, and toxin generation). Further efforts to separate oxygen effects on R_L from the complex flooding syndrome are warranted. Indeed in the few instances where several oxygen exclusion techniques have been compared factorially, plant responses have not always been uniform among modes of hypoxia. A few studies imposing hypoxic regimes or flooding have reported neutral or reverse stomatal responses (Harrington 1987; Osundina and Osonubi 1989; Pezeshki et al. 1990; Javier 1985; Thornton and Wample 1980). It was not always clear why these inconsistent results occurred although intrinsic species adaptation to hypoxia, gradual exposure allowing acclimation, exposure brevity, or undepleted oxygen regimes may have been factors in some instances.

RELATING R_L TO SOIL OXYGEN

Various parameters, including flood duration, soil gas composition and/or concentration, and soil porosity have provided reasonably good qualitative indices of plant disposition toward stomatal closure. These parameters have provided useful diagnostic criteria of anoxia, particularly for interpreting stomatal time-course response data. Using the equation form $R_L = a(ODR)^b$, where a and b are empirical coefficients, soil ODR has been the only aeration index capable of *quantitatively* predicting diffusive resistance (Sojka and Stolzy 1980; Sojka 1985).

Basing R_L prediction on ODR as the environmental descriptor ties a dynamic response of oxygen-consuming plants to an indicator of oxygen supply-rate (Stolzy and Sojka 1984). The desirability of relating respiration-linked plant responses to rate factors rather than capacity or intensity factors is well known. This approach accounts for response lags associated with dissolved oxygen depletion from flooded soil. A field study showed that 48 h of inundation were required before enough oxygen was removed by plant and microorganism respiration to lower soil ODR to the stomatal closure threshold for soybean (Oosterhuis et al. 1990a and b).

Using ODR also allows for response variations to a given soil-oxygen regime (Fig. 1.) resulting

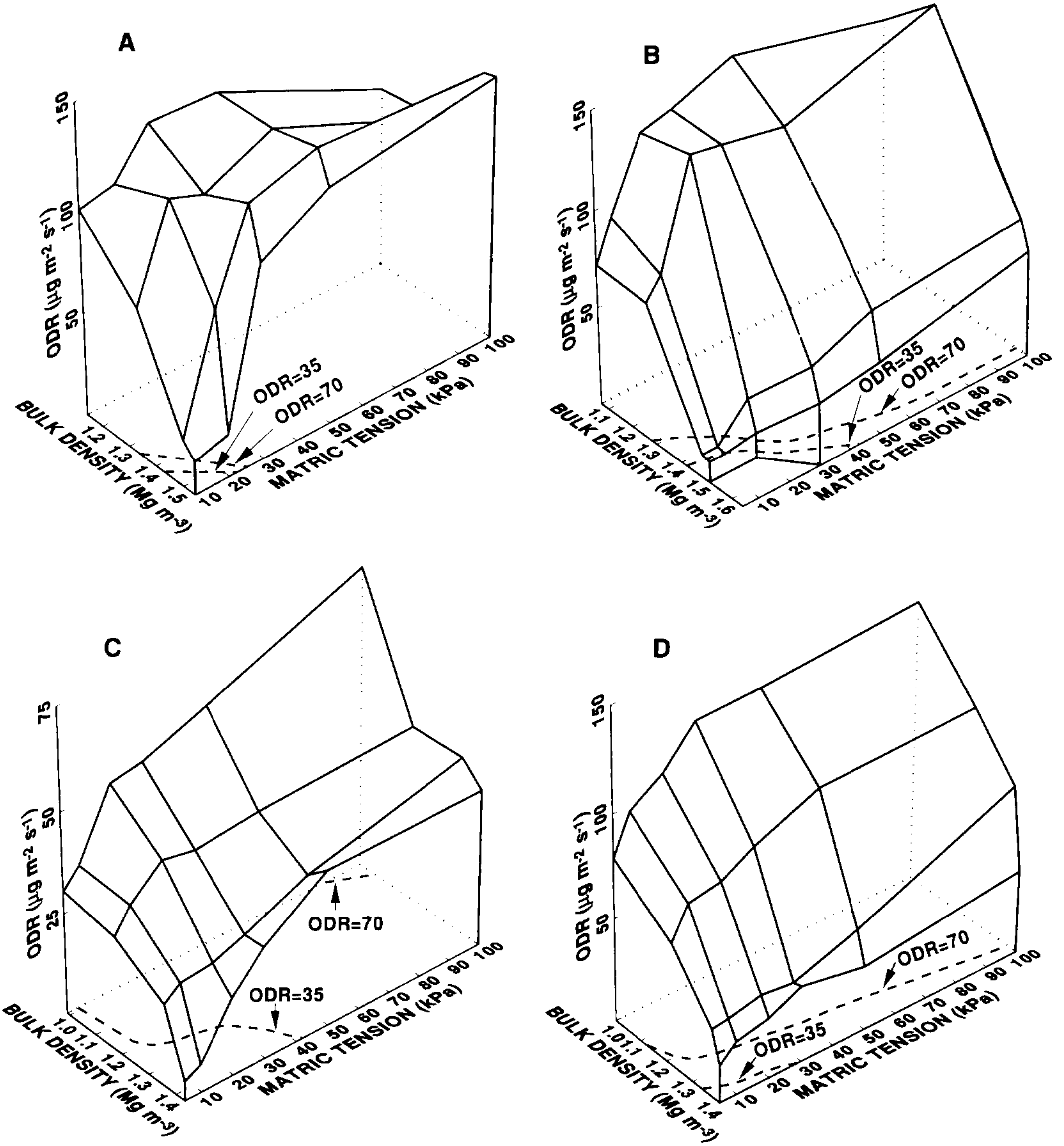

FIG. 1. Co-dependence of soil oxygen diffusion rate (ODR) on bulk density and matric tension for four soils, described originally as (a) brown soil formed from loess, (b) black earth formed from loam, (c) very heavy alluvial soil, and (d) chernozem rendzima. Dotted 35 and 70 ODR lines are flat cartesian projections of the specified rate contours, whereas complete relationships over the measured range are presented as response surfaces (adapted from Stepniewski 1980).

from the combined influence of oxygen concentration, porosity, and water content (Agnew and Carrow 1985a; Asady and Smucker 1989; Birkle et al. 1962; Holder and Cary 1984; Wilson et al. 1985; Stepniewski 1980). With increased soil temperature, ODR also accounts reasonably well for oxygen's decreased solubility in water and increased diffusion coefficients in rhizosphere water and gas components. However, as Luxmoore and Stolzy (1972) demonstrated (Fig. 2), these combined and opposing physical effects are outpaced by the change in metabolic demand for oxygen with increasing temperature.

Sojka and Stolzy (1980) combined R_L responses to a range of ODR's generated from various soil temperature × oxygen concentration combinations to describe a single R_L × ODR relationship in wheat. But using data of Reyes-Manzanares (1975) for sunflower (*Helianthus annuus*) and jojoba (*Simondsia chinensis*), each soil temperature gave a separate R_L × ODR relationship showing greater baseline stomatal closure for each progressively higher temperature (Fig 3). Similar temperature-shifted responses have been reported by Grossnickle (1987) for Spruce (*Picea sp.*) and by Donovan et al. (1989) for bald cypress (*Taxodium disticnum*) and water tupelo (*Nyssa aquatica*). Using data of Owen-Bartlett (1977), Sojka and Stolzy (1980) also found that plant age affected the relationship in cotton (*Gossypium sp*).

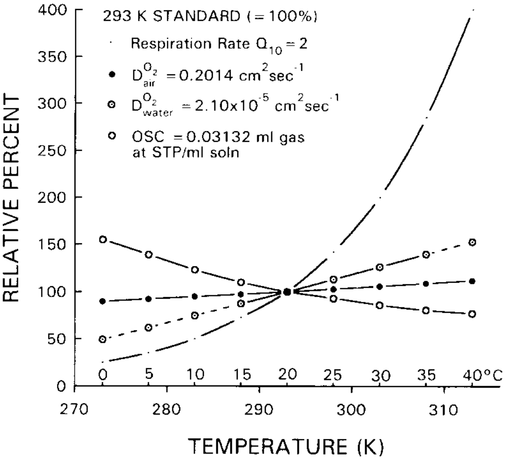

FIG. 2. Relative temperature-related changes in diffusion corn root respiration rate (assuming respiration rate doubles for each 10-K increase, i.e., $Q_{10} = 2$), diffusion coefficient (D) of O_2 in air, and in water, and O_2 solubility coefficient in water (adapted from Luxmoore and Stolzy 1972).

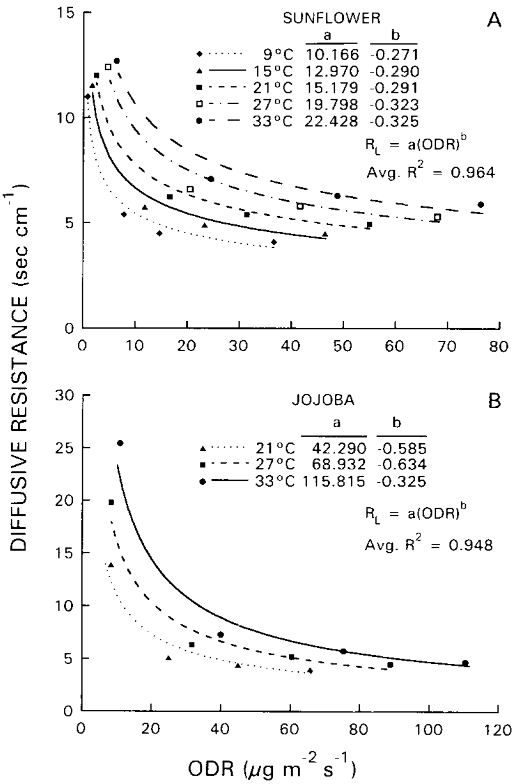

FIG. 3. Temperature dependence of the leaf diffusive resistance (R_L) × soil oxygen diffusion rate (ODR) relationship for (a) sunflower and (b) jojoba (adapted from Sojka and Stolzy (1980).

During prolonged soil anoxia or flooding the R_L × ODR relationship eventually changes, probably because of shifts to anaerobic metabolic pathways, resulting in hormonal imbalances and morphological adaptations. Gradual recovery of R_L over prolonged flooding episodes is a common observation (Fig. 4). In the case of agronomic and horticultural crops, however, conditioning seldom occurs rapidly enough to avoid catastrophic effects on crop yield and/or quality. Depending on species or cultivar hypoxia tolerance, recovery even after cessation of hypoxic conditions can take weeks and is seldom complete. This situation is made worse by a change in the base relationship between photosynthetic rate and R_L (Fig. 5). Both Oosterhuis et al. (1990a and b) and Vu and Yelenosky (1991) showed that loss of plant photosynthetic capacity was not merely a function of increased

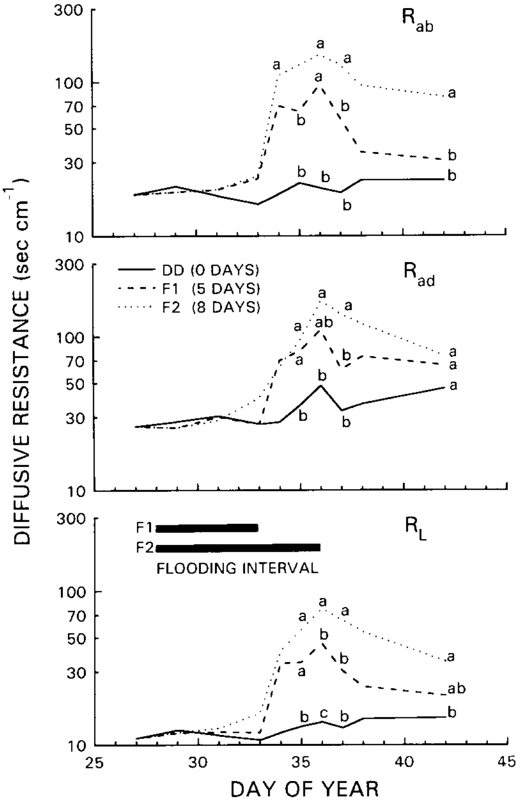

FIG. 4. Time-course of flooding effects on tomato leaf diffusive resistance (R_{ab} = abaxial resistance, R_{ad} = adaxial resistance and R_L = calculated parallel resistance), well drained (DD), 5-day flooded (F1), or 8-day flooded (F2) treatments, where flooding began on day 28. Points with differing letters on a given date in a given figure differ at $P < 0.05$ (adapted from Karlen et al. 1983).

R_L. Instead, a lower photosynthetic rate exists for a given R_L under root hypoxia compared with well aerated soil.

PHYSIOLOGICAL CAUSES

Elevation of R_L by root hypoxia is apparently the result of several interactive mechanisms. The dominance of any given mechanism varies with species, specific environmental conditions, plant growth stage, and duration and nature of hypoxia. Although attention was focussed for many years on a possible role of ethylene (Bradford and Yang 1981; Bradford et al. 1982; Pallas and Kays 1982; Aharoni 1978), and while ancillary hormonal involvement may occur (Munns and King 1988), the single mechanism that now seems most ubiquitously implicated involves accumulation of abscisic acid (ABA) in leaves during episodes of hypoxic root stress (Bradford 1983b; Jackson and Kowalewska 1983; Jackson and Hall 1987; Jackson et al. 1988; Neuman and Smit 1991; Shaybany and Martin 1977; Smit et al. 1990; Zhang and Davies 1986, 1987). There is, however, uncertainty about whether the ABA always originates in the roots or in the leaves.

During flooding, ABA apparently acts as a hormonal trigger of stomatal response. This is consistent with ABA's effect in other stressed systems (Jones and Mansfield 1972; Hiron and Wright 1973; Wright 1977; Zeevaart and Creelman 1988), particularly those exhibiting lowered plant water potentials. Examination of the studies cited in Table 1, as well as others (Schildwacht 1989; Wadman-van-Schravendijk and van Andel 1985; Zhang and Davies 1986), shows there is no consistent effect of root zone hypoxia on plant water potential, although water potentials are lowered in many instances. Increased production of ABA in root systems may initially contribute to lowering of plant water potentials by reducing root hydraulic conductivity (Markhart et al. 1979).

Aerenchyma formation (or increased root porosity) proceeds as hypoxia initiates less efficient anaerobic metabolic pathways in roots. This shift results in destruction of easily metabolized root cellular components, ultimately creating an interconnected network of gas-filled voids in the roots (Drew 1988). Abscisic acid has been shown to act as an inhibitor of maize root

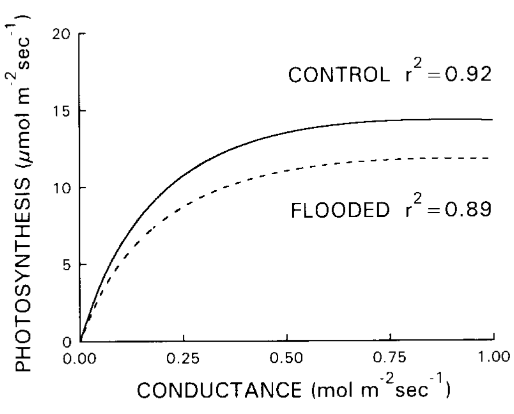

FIG. 5. Difference in the relationship between leaf photosynthetic rate and leaf conductance for flooded vs. non-flooded soybean (adapted from Oosterhuis et al. 1990).

aerenchyma formation (Konings and de Wolf 1984), which may act to prevent complete root destruction through lysigenous air space formation during anaerobic respiration. Adventitious roots, which generally have high root porosity and also help reduce flooding stresses (Javier 1985), originate above the zone of oxygen depletion.

Abscisic acid acts directly on stomatal control by impairing guard cell accumulation and/or retention of potassium ions (Mansfield and Jones 1971) and by causing transient potassium and chloride ion efflux (MacRobbie 1981). The role of ABA accumulation in leaves in response to drought stress has been widely researched (Davies and Zhang 1991). Because of the intimate involvement of potassium in guard cell turgor regulation, it is important to note that extensive reviews of plant nutritional response to hypoxia have shown that leaf, root, and whole plant potassium levels drop rapidly upon hypoxia in nearly all cases (Drew 1988; Sojka and Stolzy 1988). Potassium deficiency alone can impair stomatal opening of maize (Peaslee and Moss 1966) and reduce sugarbeet root system permeability to water (Graham and Ulrich 1972).

Nitrogen deficiency is also common in hypoxic plants, and its nutrition appears linked to stomatal regulation through an effect on ABA levels. Increased endogenous ABA was found at high plant water potentials in N-deficient cotton plants, resulting in greater stomatal sensitivity to stress (Radin and Parker 1979; Radin and Ackerson 1981; Radin 1981; Radin et al. 1982). The effects of nitrogen nutrition on stomata could not be explained by passive linkage to plant water potential. Stomata closed at higher plant water potential with nitrogen deficiency. In another group of cotton experiments, N and K concentrations fell in leaves after flooding (Reicosky et al. 1985a and b; Hocking et al. 1985). The decline in nitrogen levels corresponded to reduced growth and was associated with elevated foliage temperatures and reduced photosynthesis, which both implicate stomatal closure.

RELEVANCE AND APPLICATION

Most of the species in Table 1 are trees or woody herbaceous species, some of which are horticultural crops. One is prompted to ponder why so little attention has been paid to this phenomenon for field crops. One reason may be that as agriculture has developed worldwide, the best, least flood-prone land was the first land put into food and fiber crops, whereas more flood-prone land has remained forested longer.

Kozlowski (1984) noted that in the U.S., over 10,000 floods have been documented. In Mississippi alone, annual flooding can cover 1.6 million ha. Thus, both flood numbers and extent of flooding may rival the occurrence of serious drought. Localized crop devastation from floods is often associated with storms, many of which go unrecorded as "official" flood events. In addition, poor soil aeration and perched or shallow water tables occur frequently outside the context of meteorological flooding. Fine textured soils, potholes, internal drainage to footslopes, and excess irrigation without adequate draining expand the scope of hypoxia. The experiences of U.S. cornbelt farmers in the Spring of 1991 bore witness to the calamitous consequences of hypoxic stresses and the lack of adequate strategies for dealing with them. Where the previous year's summer-long droughts had substantially reduced yields gradually over months, a week or 10 days of flooding in the spring of 1991 resulted in crop failure for extensive areas.

Box (1986) demonstrated that prolonged periods of ODR sufficiently low to cause stomatal closure in wheat is a common occurrence in the wheat double-cropping region of the southeastern U.S. and may be a major factor contributing to the region's depressed yields. Scott et al. (1989) demonstrated increased yield-loss susceptibility to flooding in field-grown soybean stressed for fixed durations at progressively more mature plant growth stages.

As Fig. 4 demonstrates, stomatal recovery from hypoxia is usually slow and incomplete. Flooding episodes represent significant periods with little or no net photosynthetic gain and are often associated with necrotic root pruning and permanent root impairment, disease, or foliar necrosis, leaving crops susceptible to damage from subsequent stresses. Stomatal responses are ultimately reflected in yield and/or quality reductions.

A conceptual comparison of the effects on yield potential of flooding vs. drought stress is proposed in Fig. 6. Hypoxic stress can often impact crop yield potential more perniciously than drought stress. Drought-stressed crops usually accrue a slow linear reduction in yield po-

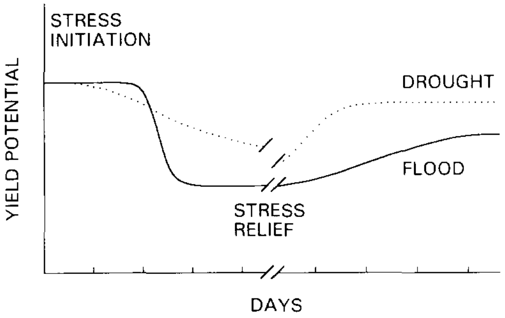

FIG. 6. Conceptual comparison of stress accumulation and stress relief effects on yield potential for flooding stress vs. drought stress.

tential over the stress episode. If the crop is not strongly determinate and if stress does not occur at a critical growth stage, substantial recovery of yield potential may result when water is again available. Contrastingly, hypoxic stress, after a brief lag associated with rhizosphere oxygen depletion, usually results in rapid sharp reduction of yield potential, generally with only gradual and poor recovery of yield potential upon reintroduction of oxygen into the root zone.

Stomatal closure and recovery patterns under hypoxia deserve greater attention in dynamic crop modeling. Even the limited existing data from field crops reviewed in this paper provide significant insight. Critical model components should include response lags associated with initial profile oxygen depletion, loss of photosynthetic capacity, reduced root metabolic efficiency, duration of hypoxia, root temperature, plant age and growth stage effects, and gradual recovery to near-normal functioning.

Interactions of these factors impinge on a number of critical questions. The extent to which onset of stomatal dysfunction during soil hypoxia affects the temperature of well watered canopies as a function of ambient vapor pressure deficit has not been documented. Documentation of these effects may prove challenging because of the lack of correlation that is often found between plant water potential and R_L during hypoxic episodes (Bradford 1983a; Bradford and Hsiao 1982; Davies et al. 1987; Everard and Drew 1989; Neuman and Smit 1991; Sojka and Stolzy 1980). These relationships may be affected by confounding hormonal controls of stomatal movement, alteration of nutrient fluxes to and from guard cells, or even diffusion of elevated levels of CO_2 through roots of flooded plants to leaves, affecting stomatal performance.

Stomatal measurements in field crop management studies targeting potentially hypoxic soil environments might provide a sensitive indicator of stress. Preliminary studies may be required to determine the extent to which problems surrounding measurements of R_L (Idso et al. 1988, 1989; Monteith 1990) are diminished or exacerbated with stomatal closure in response to stimuli other than drought. Stomatal monitoring could provide an excellent physiological diagnoses of occurrence, severity, and duration of oxygen stress episodes.

As in dealing with all other environmental stresses, breeding for resistant crops would probably provide a potent problem solution. Measurement of leaf diffusive resistance or its reciprocal, leaf conductance, in controlled hypoxic environments provides sensitive comparisons of species stress resistance; conceivably, this approach could be used for cultivar comparisons as well. In this vein, research is warranted to determine the degree of correlation between root aerenchyma formation and recovery of stomatal function.

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