17 Root Oxygen Deprivation and the Reduction of Leaf Stomatal Aperture and Gas Exchange

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I. INTRODUCTION

The most ubiquitous plant abiotic stress in the global environment is generally thought to be water deficit. The opposite of water-deficit stress, flooding, initially involves relief of the abiotic factor of water deficit and only becomes stressful after flooding persists long enough to directly or indirectly interfere with a variety of plant functions via several mechanisms. The relief of stress with short term flooding (typically a day or less) is the principle upon which irrigation hinges. By contrast, the negative impacts of prolonged flooding on ecosystems, and particularly agricultural production systems, are substantial [1] and may be as significant as drought, depending on one's accounting strategy. Much of this impact is the result of the combination of soil and plant chemical, physical, and biological changes that cause stomata to close after prolonged flooding. This contributes significantly to a drastic reduction in photosynthesis and damages many other plant functions by disrupting

transpiration and the complex system of hormonal control of plant systems and processes.

Figure 17.1 gives a conceptual diagram of the effects of flooding on the yield potential of a crop and compares the pattern with what is typically seen under drought. With drought stress, onset is very gradual and plant adaptation has ample time to occur at a pace that moderates the impact of the water-deficit stress. Drought would have to persist for weeks in most crops to collapse the yield potential to near-zero levels. Unless water-deficit stress is exceedingly severe and has persisted for weeks, the loss in yield potential is moderate, and relief of the stress can usually bring about substantial recovery in yield potential, even full recovery, although yield components may shift. By contrast, when flooding occurs, plants initially see relief of any water deficit stress they may be experiencing. However, as the oxygen in the root zone is depleted by plant roots and competing soil organisms (usually in the first 24–48 h), the initial boost in yield potential rapidly gives way to a
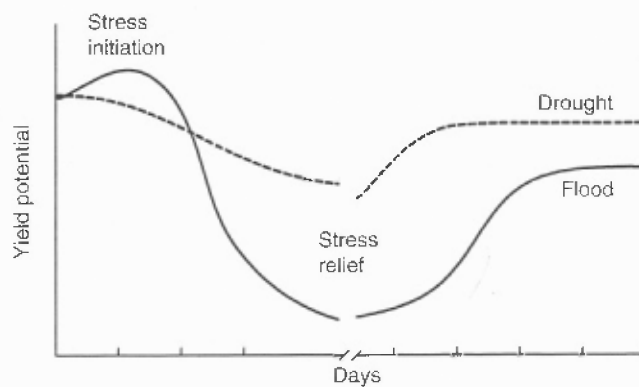
FIGURE 17.1 Conceptual comparison of stress accumulation and stress relief effect on yield potential for flooding stress vs. drought stress.

precipitous drop. Stress relief upon drainage typically produces a far more gradual, and usually less successful recovery than with moderate drought, simply because the plant infrastructure is often far more devastated by the many system impairments that can accumulate with flooding. In our chapter, reference to flooding in the context of this subject matter refers to prolonged flooding, typically 24–48 h or longer, which is about the length of time usually needed for soil organisms to deplete soil water of dissolved oxygen.

It is interesting and curious that common plant reactions to root inundation or prolonged flooding involve several physiological responses much akin to drought stress. This occurs even though plant roots are submerged, i.e., in contact with free water. That wilting and stomatal closure occuring in flooded plants indicate that the physiological responses to flooding are not caused by the energy status of the water, which is the dominant direct mechanism initiating wilting and stomatal closure during drought. The physiological responses to soil hypoxia and flooding have been reviewed by a number of scientists [1–5].

The wilting, stomatal closure, and various other physiological responses to flooding have been explained by several plant response scenarios. These fall into about five categories: obstruction of xylem elements by disease organisms, reduced root system extent or root system/membrane water conductance, altered soil–plant nutritional status, production or imbalancing of plant hormones or biochemical signaling compounds, and the action of soil- or plant-produced toxins [2,6–11].

II. FLOODING AND HYPOXIA EFFECTS ON SOIL PROCESSES

The way in which flooding or waterlogging proceeds along a given scenario or set of scenarios is related to how the physical and chemical properties of water affect soil mineral and biological processes. Ponnamperuma [12] gave an excellent summary of the physicochemical processes that occur in soil upon prolonged flooding, depleting oxygen as an electron acceptor. As reactive oxygen disappears, soil redox potential falls, causing a cascading series of organic and mineral transformations, resulting in the release of numerous soluble chemically reduced minerals, many of which are toxic to plants including methane, sulfides, and reduced forms of iron and manganese.

Water is essential to most soil biological activities. As the amount of water in the soil environment shifts from shortage to plentiful and on to excess, the populations and functional dominance of competing organisms also shift. Under excessively wet or flooded conditions, disease organisms are often favored [8]. Water affects the heat capacity, heat conductivity, and evaporative properties of soil in a way that generally tends to cool soil when wet. Water is a potent solvent, facilitating the mobility of mineral and organic solutes, to the benefit or detriment of a given soil biological process, depending on the intensity and direction of solute movement into or out of an organism's sphere of influence.

Very important to our discussion is the fact that water also changes the net oxygen availability of the soil environment in a temperature-dependent fashion. While soil aeration can be characterized as the volume of gas-filled pore space in a given soil volume, or as the concentration of oxygen (and other gases) within the pores, most edaphologists agree that soil oxygen diffusion rate (ODR) is the best indicator of soil aeration status. This is because ODR gives an indication of the soil's ability to supply oxygen to organisms as a rate function [13]. Rhizosphere ODR is also relatively easy to determine using the platinum microelectrode technique [14,15], and leaves both soil and roots essentially undisturbed. The rate at which soil can supply oxygen must be balanced against the rate at which an organism in soil consumes oxygen. This balance of rates has been the basis of understanding and modeling soil-oxygen-mediated pro-
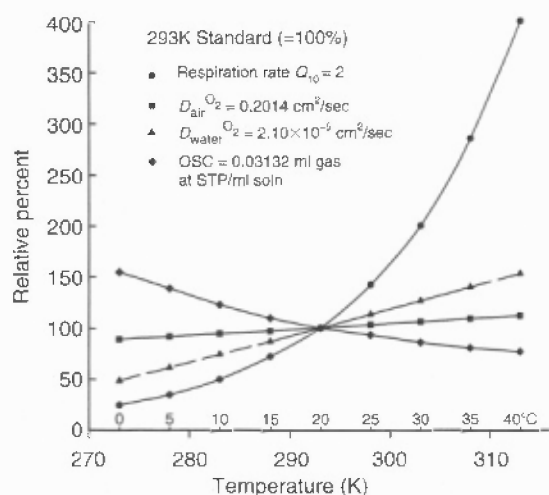
FIGURE 17.2 Relative temperature-related changes in corn root respiration rate (assuming respiration rate doubles for each 10 K increase, i.e., $Q_{10} = 2$), diffusion coefficient (D) of O_2 in air and in water, and O_2 solubility coefficient (OSC) in water. (From Ref. [9], as adapted from Refs. [17,18].)

cesses [16,17]. Luxmoore and Stolzy [18] gave an elegant graphic depiction of this dependency (Figure 17.2).

As soil water content increases, the thickness of water films around soil particles, microorganisms, and surfaces of plant roots also increases. The thickness of these water films greatly influences the transfer of oxygen from the soil environment to respiration sites in roots and microorganisms [8]. Oxygen diffuses 10^4 times more slowly through water than through air [19] and only one-fourth as rapidly through dense protoplasm as through water [20,21]. The physics of this process are described by Fick's first law:

$$J = D_0 \ dC_0/dx$$

where J is the gas flux per unit cross sectional area of soil, C_0 is the concentration of the particular gas in the gas phase of the medium, and D_0 is the apparent diffusion coefficient of the gas in the medium [22,23].

There is a long history and voluminous literature pointing to the direct and indirect roles of rhizosphere oxygen status during flooding as key factors in plant physiological response to flooding. Clements [24] documented that the negative impacts of waterlogging on plants have been recognized for centuries. The specific role of soil oxygen for maintaining plant vigor was noted as early as 1853 [25]. Rhizospere oxygen status appears to affect plant physiological responses both directly (via respiration-mediated metabolic processes in the root) and indirectly (via cascading chemical, biochemical, and physical processes in the soil, rhizosphere, and the plant).

Our chapter focuses primarily on the role of root zone hypoxia and anoxia in bringing about stomatal closure. While flooding or waterlogging is certainly the most common circumstance limiting root oxygen availability, it is not the sole scenario. Several other examples can be noted. Generous incorporation of fresh organic matter into warm wet soil can stimulate depletion of soil oxygen through the respiration of microorganisms decomposing the fresh substrate. Soil compaction, which reduces average gas-filled soil pore size and total pore space of soil, creates many dead-end soil pores, and favors blockage of the smaller soil pores with water films, restricting diffusion of oxygen through the soil matrix. Oxygen diminishes with soil depth, and if an established plant's roots are buried too deeply under additional soil, the root system can become oxygen limited.

The dominant literature, of course, relates to flooding; however, a number of studies have manipulated soil oxygen independently of flooding, providing important insights to the phenomena [8]. Also, since oxygen unavailability is probably the dominant direct trigger for most of the plant responses that ultimately manifest themselves as familiar visual and otherwise easily monitored physiological responses, it is logical to quantitatively tie measurable physiological responses to rhizosphere ODR values. ODR can be physically predicted with reasonable reliability for a range of soil conditions [26–28]. Thus, the correlation of quantifiable physiological responses to ODR measurements facilitates the normalizing of responses to a reliable soil indicator, allowing species and cultivar response comparisons. Ultimately this approach also enables modeling of physiological responses on a sound physical basis.

In contrasting the effects of flooding and other sources of oxygen exclusion, it is important to remember that flooding causes numerous ancillary changes in the rhizosphere. These include lowered chemical redox potential, resultant specific ion effects, leaching of mobile water-soluble nutrients, metabolic release, and dispersal from microorganisms of organic compounds affecting higher plant function, displacement of soil oxygen with carbon dioxide, ethylene, and other partially water-soluble plant-impacting gases, and promotion of favorable conditions for pathogens. When they occur *en suite*, these multiple rhizosphere changes confound our ability to understand stomatal closure, which so strongly impacts gas exchange and photosynthesis. Direct manipulation of soil atmospheres has been used in many experiments to limit the sources of confounding, and/or reduce their intensity.

III. SOIL HYPOXIA, THE RHIZOSPHERE, AND PLANT METABOLISM

As the rate of oxygen supply dwindles in a soil system, eventually falling below the demand rate of respiring organisms, a series of consequences often results. Initially, root respiration, lacking sufficient free oxygen, begins to proceed along a fermentative pathway, rapidly consuming the available pool of stored carbohydrates in what is often referred to as the Pasteur effect [29–31]. Under these conditions, oxidative phosphorylation of mitochondria is blocked and the Krebs cycle is bypassed in meeting the demand for adenosine triphosphate (ATP) [32]. Alcohol, rather than carbon dioxide, becomes the dominant metabolic by-product released. The relative amount of energy released in this manner is only about 5% of that liberated by substrates utilized via the aerobic respiration pathway [29]. There can be numerous other alternative pathways, depending on the organism and properties of the soil system [31]. These include reduction of inorganic compounds such as sulfur and production of other by-products, such as methane. The specific biochemical pathways taken under hypoxic conditions probably varies among higher plant species and their complexities are not yet fully understood [33–37]. Several authors have suggested that the alcohol produced under hypoxic conditions does not injure roots because it easily migrates out of and away from the root and perhaps the action of acetaldehyde, rather than alcohol is the injury causing agent in these scenarios [38].

Boamfa et al. [39] showed that oxygen released by photosynthesis in rice (*Oryza sativa*) was completely consumed within the plant and that exposure to light reduced the intensity of the anaerobic metabolic responses. By contrast Luxmoore et al. [16] showed an increase in root porosity and hypoxic symptoms in oxygen-stressed wheat (*Triticum aestivum*) exposed to increasingly higher light intensities. It was their interpretation that under high light intensity there is a large supply of carbohydrate to the root, a high respiration rate, and an "induced oxygen scarcity" to inner root cells resulting in necrosis of some cells and the development of gas spaces.

Generally, as aerobic respiration becomes impaired, energy conversion slows and potentially toxic organic and inorganic wastes begin to accumulate in the rhizosphere and in the plant, impairing various metabolic and membrane functions, particularly in roots. Flooded plants also tend to produce fewer mycorrhizal filaments affecting nutrient and water availability as well as extent of contact surface for diffusion entry of oxygen [40,41]. As a result, in the early stages of root hypoxia, root uptake of nutrients from soil slows and plants begin to experience mobilization and reallocation of existing nutrients from areas of higher concentration (usually from actively growing, more juvenile tissue) to areas of lower concentration [42–44]. Passive transfer of water and nutrients in the xylem stream is also reduced as stomata close and transpiration decreases.

Reviews of physiological response to flooding or hypoxia have usually noted that there is not a consistent co-occurrence of plant water potential shift associated with hypoxia-induced stomatal closure. Even when changes in water potential accompany stomatal response, it is often not clear whether stomata are more directly affecting or affected by the changes in plant water potential. Because of the complicated nature of these environmental alterations and the equally or greater complexity of species-specific plant response to each given hypoxia-dominated scenario, it may well be that different processes dominate under different circumstances.

Eventually with prolonged hypoxia, because energy conversion has become so inefficient, the substrate requirement of roots can only be met by metabolizing less resistant cellular constituents in place. This latter process gradually results in the development of lysigenous zones of intercellular voids, which eventually contribute to improved internal diffusion of oxygen to the roots from the aerial portions of the plant. This constitutes one of the most important adaptive mechanisms of flood resistant plants, allowing survival and eventual return to more normal plant function [16–18,45–58].

If a plant is less capable of shifting metabolic pathways, or if hypoxia persists and the entire soil profile is completely depleted of oxygen, resulting in hypoxia or anoxia that persists for several days, root systems become necrotic. Necrotic tissues lose physical integrity and can provide an easy vector for pathogen and pest invasion. This process, which is sometimes referred to as root pruning, also impairs physiological recovery following improved aeration of the profile — for example, upon drainage following flooding. In this case root extent has been abruptly decreased making plants far more susceptible to subsequent water deficits. The increase in root-to-shoot ratio impairs soil-nutrient and soil water extraction and slows the recovering plant's subsequent growth. In crop plants this usually significantly reduces crop yield [59–67].

IV. HYPOXIA AND STOMATAL CLOSURE

The effect of flooding on stomatal closure has been recognized directly or indirectly for at least 60 years, however, only a few papers have concentrated on soil

oxygen effects per se. Reduced transpiration and photosynthesis was seen by Childers and White [68] within 2 to 7 days of flooding apple trees (*Malus domestica*). They reported slight elevation of transpiration and photosynthesis immediately upon inundation, likely due to initial relief of mild water-deficit stress. But, as in many findings to the present day for many species, after about 48 h leaf expansion ceased and root necrosis became extensive. While their measurements showed no leaf temperature or stomatal aperture differences among treatments, this failure may have been the result of inadequate measurement technology at the time of their work. Reduced stomatal conductance and photosynthesis in soybean (*Glycine max*) 2 days after flooding imposition was reported by Oosterhuis et al. [60,61].

Moldau [69] published the first measurement of increased leaf diffusive resistance (R_L), which is the inverse of leaf conductance (g_s), caused by root waterlogging in common bean (*Phaseolus vulgaris*). Smucker [70] also reported similar findings for navy beans. Regehr et al. [71] reported increased R_L for flooded cottonwood (*Populus deltoides*). Meek et al. [72] reported that R_L was greater for cotton (*Gossypium hirsutum*) with a continuous 30 cm water table depth than with a 90 cm depth, and also noted reduced soil ODR in wetter profiles. These early measurements of increased R_L drew attention to waterlogging's impairment of normal plant control of leaf gas exchange and regulation of water and solute transport. These reports also explained earlier observations of reduced leaf damage by airborne oxidants when exposure occurred during flooding [73,74].

Increased R_L in wheat (*Triticum aestivum*) was measured by Sojka et al. [75] when the wheat was grown at optimal water content but had soil oxygen excluded by continuous flushing of the soil with mixtures of air and nitrogen gas (Figure 17.3). Flushing with ambient air (21% O_2) had the lowest R_L, flushing with pure N_2 produced the highest R_L, and flushing with a 4% oxygen concentration only slightly increased R_L over the air-flushed treatment. In subsequent publications [9,76–78] curvilinear regression demonstrated that R_L could be reliably related to measurements of soil ODR as measured by the platinum microelectrode technique [14] for a number of diverse plant species grown at optimum water contents in controlled soil oxygen chambers. This pattern suggested that stomatal response to soil oxygen availability was abrupt at some threshold value of oxygen availability. The curvilinear regressions of R_L against ODR for numerous species have shown sharp response thresholds occurring at or near ODR values of 20×10^{-8} g/cm^2/min. This same ODR value is a
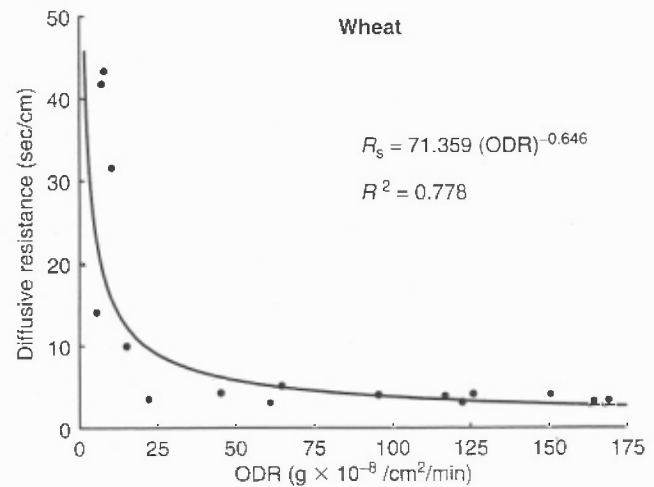

FIGURE 17.3 Diffusive resistance of wheat flag leaves as affected by soil oxygen diffusion rate (ODR). (From Sojka RE, Stolzy LH. *Soil Sci.* 1980; 130:350–358. With permission.)

recognized threshold for a variety of plant growth, physiological and nutritional responses [8,79].

The observations from controlled root atmosphere chambers also suggested that stomatal closure from reduced oxygen in the root zone was largely independent of increases in rhizosphere carbon dioxide or other physiologically active gases such as ethylene. Even though those gases were not measured in the studies, they could not have accumulated significantly in the soil because of the continuous flushing of the root chambers with gas mixtures free of the suspect gases. While various power or exponential equations could provide high correlation of R_L to ODR for a given study, the equation form of the curvilinear relationships observed in these root-gas studies that most often worked well across species and studies was the simple power function:

$$R_L = a(\text{ODR})^b$$

As Figure 17.4 shows, there was also an interaction of stomatal response with root temperature. As root temperature increased, the baseline R_L increased. This would be expected, since as we learned in Figure 17.1 that the respiration requirement increases with temperature. Thus, the adequacy of oxygen availability for roots or root-linked plant functions at any given soil ODR diminishes as temperature in the root environment rises, increasing the demand side of the two rate functions. The expression of this dependency in Figure 17.4 is the increase in R_L with root temperature.
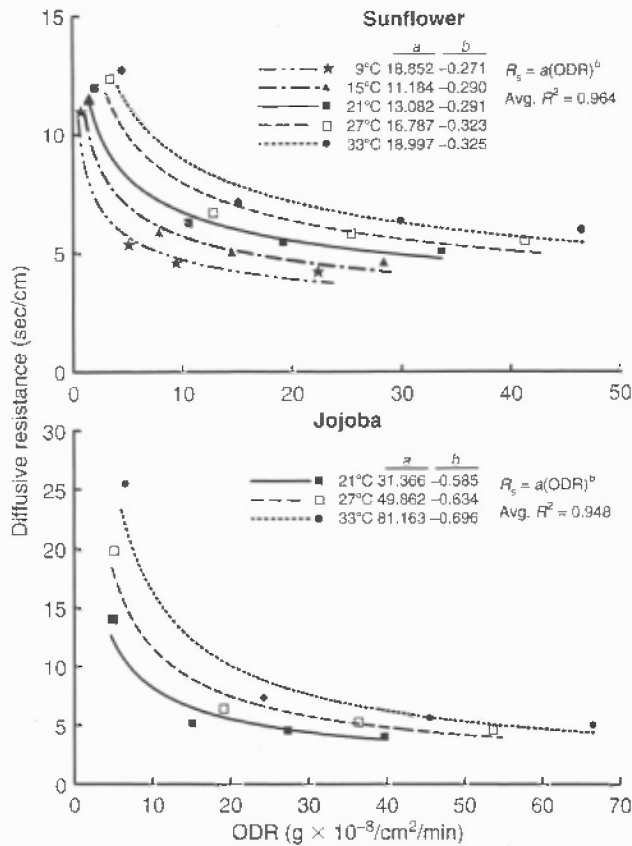
FIGURE 17.4 Leaf diffusive resistance (R_s) as a function of soil oxygen diffusion rate (ODR) at various soil temperatures for sunflower and Jojoba. (From Sojka RE, Stolzy LH. *Soil Sci.* 1980; 130:350–358. With permission.)

FIGURE 17.5 Time-course of flooding effects on tomato leaf diffusive resistance (R_{ab} = abaxial resistance, R_{ad} = adaxial resistance and R_L = calculated parallel resistance). Flood treatments were well drained (DD), 5-day flooded (F1), or 8-day flooded (F2), where flooding began on day 28. Points with differing letters on a given date in a given figure differ statistically at $P < 0.05$. (From Ref. [9] as adapted from Ref. [80].)

In the series of investigations conducted by Sojka and Stolzy, cited above, the value of R_L regressed against ODR was the parallel resistance calculated from the individual adaxial (R_d) and abaxial (R_b) leaf measurements, using the relationship

$$R_S^{-1} = R_{ab}^{-1} + R_{ad}^{-1}$$

In a flooding study of tomato (*Lypersicon esculentum*), Karlen et al. [80] showed that, while adaxial surfaces of control plant leaves had somewhat higher diffusive resistance values than their abaxial surfaces, the diffusive resistance response to flooding regimes of either individual surface or of the calculated parallel resistance were similar in pattern and magnitude (Figure 17.5). One difference was a faster recovery to a normal resistence value for adaxial leaf surfaces.

Figure 17.6 and Figure 17.7 show the stomatal response of soybean (*Glycine max*) to reduction in root zone oxygen availability [78]. Figure 17.6 shows a series of vinyl leaf surface impressions associated
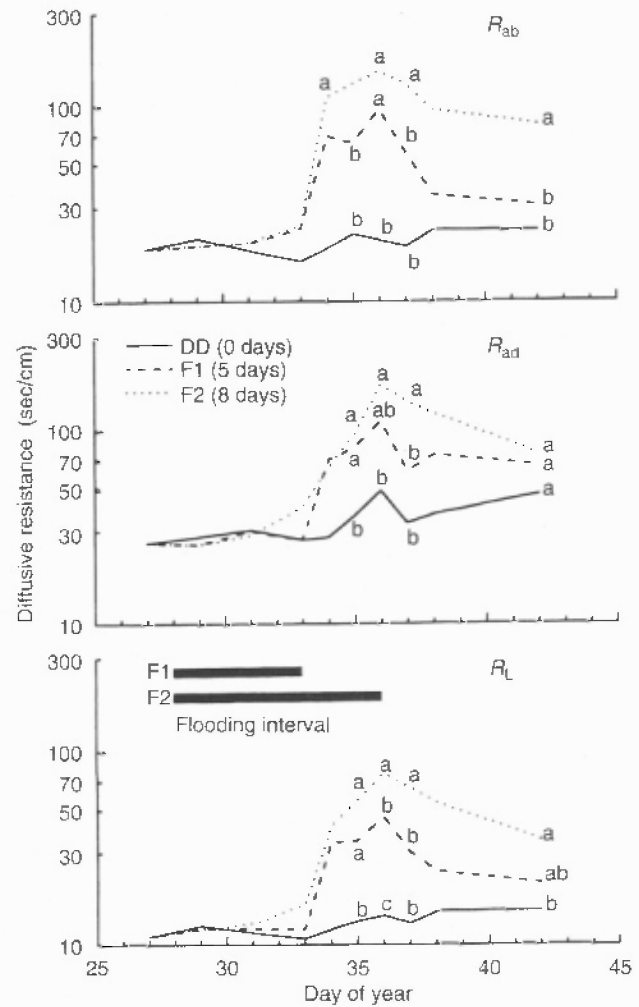
with continuous flushing with varying oxygen mixtures through the sealed cylinders in which the soybean root systems were growing. Figure 17.7 gives the R_L and ODR values generated by the treatment scheme. A key finding of this study was that the R_L increase in the poorly aerated treatments were not due to changes in the stomatal number per unit leaf area. This finding is not entirely consistent among reports of stomatal closure with flooding in the literature. The effect of hypoxia on stomatal distribution and function is likely species dependent and, perhaps more importantly, dependent upon the onset history of flooding treatments. Plants that
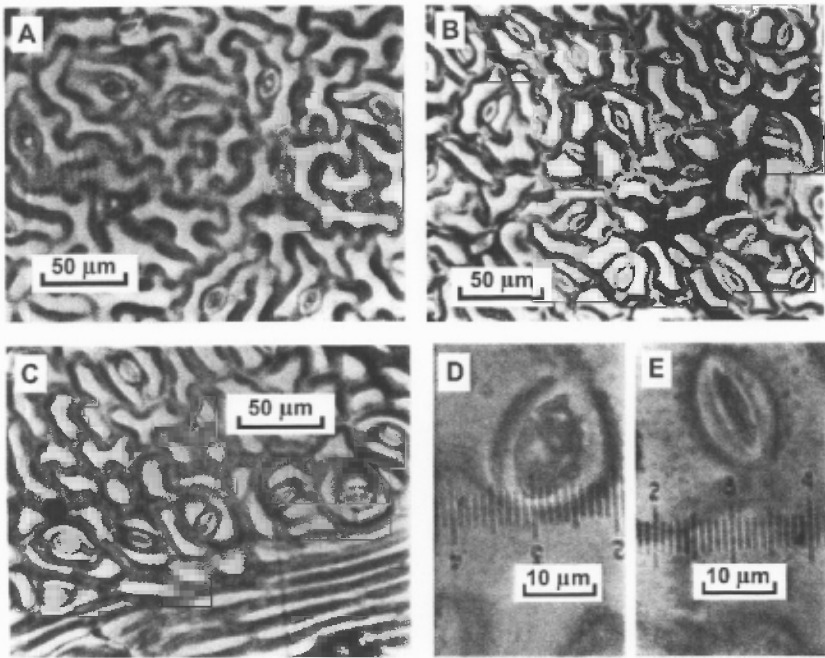
FIGURE 17.6 Photomicrographs of vinyl leaf impressions showing: (A) open, well-aerated (21% O_2) abaxial stomata; (B) closed, more densely distributed abaxial stomata of the poorly aerated (0% O_2) treatment; (C) grouping of adaxial stomata along leaf xylem; (D) enlarged impression of an open (21% O_2) stomate and (E) enlarged impression of a closed (0% O_2) stomate. (From Sojka RE. *Soil Sci.* 1985; 140:333–343. With permission.)
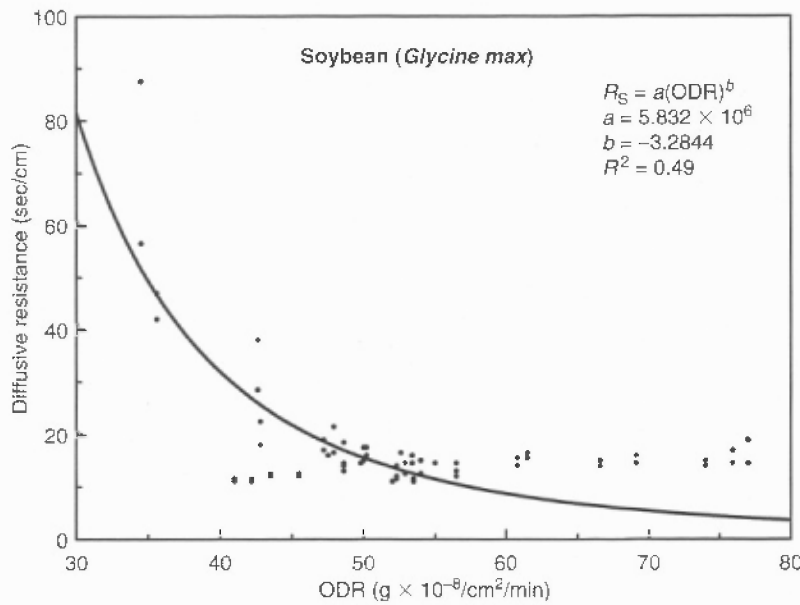

FIGURE 17.7 Parallel leaf diffusive resistance (R_S) as a function of soil oxygen diffusion rate (ODR) measured on several observation dates. Each point is the mean of between 3 and 12 observations. (From Sojka RE. *Soil Sci.* 1985; 140:333–343. With permission.)

are abruptly stressed would have no opportunity to experience changes in leaf expansion or cell differentiation affecting R_L or g_s, and any response in these parameters would have to be physiologically driven rather than morphologically driven. Gradual or repeated onset of stress would provide an opportunity for morphological differentiation. Greater R_L or reduced g_s caused by changes in stomatal distribution or dimensions would have to result from a drop in stomatal density or a reduction in stomatal (i.e., guard cell) size. These morphological changes in response to growth-inhibiting stress scenarios have rarely been reported.

There have been extensive observations of increased leaf diffusive resistance, or decreased leaf conductance across scores of plant species (Table 17.1). Not all studies specify whether the resistances reported are abaxial, adaxial, or parallel resistances. Among the studies where abaxial and adaxial responses are observed separately, the most common occurrence is a general similarity of abaxial and adaxial response. However, some cases of surface-

TABLE 17.1

Observed Increase of R_L or Decrease of g_s in Response to Root Flooding or Hypoxia

Species	Stimulus	Refs.	Species	Stimulus	Refs.
Acer rubrum	Soil O_2 + CH_4	[129]	Phaseolus vulgaris	Flood	[69,181–183]
Acer rubrum	Flood	[130]		Anoxic soln.	[127,182–185]
Acer saccharum	Soil O_2 + CH_4	[129]	Picea glauca	Flood + heat	[186]
Actinidia chinensis	Flood	[132]	Picea gauca	Flood	[165]
	Anoxic soln.	[132]	Picea mariana	Flood + heat	[186]
Actinidia deliciosa	Flood	[133,134]	Picea mariana	Flood	[164]
Apios americana	Flood	[135]	Pisum sativum	Flood	[103,187–189]
Avicennia germinans	Flood	[136]	Poa pratensis	Compaction +	[190]
Avicennia marina	Flood	[137]		irrigation	
Betula papyrifera	Flood	[138]	Populus balsamifera	Flood	[191]
Betula nigra	Flood	[138]	Populus canadensis	Flood	[191]
Betula platyphylla	Flood	[139,140]	Populus deltoides	Flood	[71,81]
Bruguiera gymnorrhiza	Flood + salt	[128]	Prioria copaifera	Flood	[156]
	Flood	[137,141]	P. trichocarpa × deltoides	Anoxic soln.	[128,192,193]
Citrus aurantium	Flood	[94,142]	Prunus armeniaca	Flood	[194]
Citrus jambhiri	Flood	[94,142]	Prunus cerasus	Flood	[115]
Citrus sinensis	Flood	[142]	Prunus persica	Anoxic soln.	[147]
Capiscum annuum	Flood	[143]		Flood	[91,175,195]
Carya illinoensis	Soil O_2	[144]	Pyrus betulaefolia	Anoxic soln.	[147,196]
	Flood	[82,145]		Flood	[91]
Cucurbita pepo	Flood + salt	[146]	Pyrus calleryana	Anoxic soln.	[147,196]
Cydonia oblongs	Anoxic soln.	[147]		Flood	[91]
	Flood	[91]	Pyrus communis	Anoxic soln.	[147,196]
Eucalyptus	Flood	[81,148]		Flood	[91,174]
camaldulensis			Pyrus pyrifolia	Flood	[91]
Eucalyptus globulus	Flood	[81,148]	Pyrus ussuriensis	Flood	[91]
Eucalyptus obliqua	Flood	[148]	Quercus alba	Flood	[149]
Fraxinus pennsylvanica	Flood	[81,149–152]	Quercus falcata	Flood	[197,198]
Glycine max	Flood	[60,61]	Quercus lyrata	Flood	[198]
	Soil O_2	[78]	Quercus macrocarpa	Flood	[152]
Gmelina arborea	Flood	[153,154]	Quercus nigra	Flood	[149]
Gossypium barbadense	Soil O_2	[76,155]	Quercus michauxii	Flood	[83]
Gossypium hirsutum	Flood	[72]	Quercus nuttallii	Flood	[83]
	Soil O_2	[76,155]	Quercus rubra	Flood	[81]
Gustavia superba	Flood	[156]	Rhizophora mangle	Flood	[136]
Helianthus annuus	Anoxic soln.	[157]	Rhizophora mucro nata	Flood	[137]
	Flood	[158,159]	Salix discolor	Anoxic soln.	[147]
	Anoxic soln. + salt	[160,161]		Flood	[91]
	Soil O_2 + heat	[76,77,162]	Salix nigra	Flood	[81]
Hydrangea macrophylla	Flood	[163]	Simmondsia chinensis	Soil O_2 + heat	[76,77,162]
Larix laricina	Flood	[164,165]	Sorghum bicolor	Flood	[159]
Liquidambar styraciflua	Flood	[166]	Taxodium distichum	Flood + salt	[85]
Lycopersicon esculentum	Flood	[80,102,167–171]	Tectona grandis	Flood	[154]
Mangifera indica	Flood	[172,173]	Theobroma cacao	Flood	[199]
Malus domestics	Flood	[91,174,175]	Triticum aestivum	Soil O_2 + heat	[75–77]
Melaleuca quinquenervia	Flood	[176]		Anoxic soln.	[200]
Momordica charantia	Flood	[177]	Ulmus americana	Flood	[81,201]
Nauclea diderrichii	Flood	[154]	Vaccinium ashei	Flood	[93,202]
Nyssa aquatica	Flood	[149]	Vaccinium corymbosum	Flood	[92,203,204]
Nyssa aquatica	Flood + heat	[178]	Virola surinamensis	Flood	[156]
Panicum antidotale	Flood + salt	[179]	Vitis sp.	Flood	[175]
Persea americana	Flood	[180]	Zea mays	Anoxic soln.	[183,205]

differentiated onset or recovery of stomatal response to hypoxia or flooding have been reported among species with varying degrees of surface differentiation [80–82].

In rare instances, prolonged flooding has been associated with reduced R_L or increased g_s, usually in highly specialized plants, such as bald cypress (*Taxodium distichum*) or rice (*Oryza sativa*), which are specifically adapted to flooded environments [83,84]. We have not attempted to comprehensively catalogue these exceptions, which are not always consistent, even for the particular adapted species [85], but have found a few reports for several species [86–90]. It is not always clear what caused these responses, although factors may include intrinsic species adaptations to hypoxia, gradual exposure allowing adaptation, exposure brevity or an undepleted oxygen supply.

V. STOMATA CLOSURE MECHANISMS

While there is not yet a complete understanding of the physiological and biochemical mechanisms that bring about stomatal closure, several processes are repeatedly implicated in the published literature. A number of studies have shown increased root resistance to water entry to meet transpirational needs [91–94]. This may be the result of loss of root hairs or microrrhiza as hypoxia persists, or changes in membrane properties reducing the hydraulic conductivity of roots. With prolonged flooding disease entry may physically block xylem elements [8].

Potassium ion flux is crucial to regulation of guard cell turgor. Several researchers [9,78,95,96] noted that the single most consistent nutritional shift reported for plant hypoxia and flooding is a drop in leaf or plant potassium concentration. While reviews of nutritional involvement in root hypoxia have noted that several other plant nutrients, particularly nitrogen and phosphorus are often impacted [96], the consistency of response and directness of cause–effect relationship, particularly in the response time frame of stomatal closure is less clear. Because potassium accumulation and retention is an active uptake process requiring outlay of energy [97], it is rapidly disrupted when anaerobic respiration ensues and plants become energy-starved. Loss of potassium ion in the leaves is thought to impair the function of the potassium ion pump responsible for maintaining the turgor of guard cells that opens stomatal pores for gas exchange between the atmosphere and the leaf interior. Peaslee and Moss [98] showed that potassium deficiency alone can impair stomatal opening of corn (*Zea mays*), and Graham and Ulrich [99] showed potassium deficiency reduces sugarbeet root system permeability to water.

Many observations of stomatal closure with root hypoxia or flooding have noted increases in leaf abscisic acid (ABA) concentrations, with the ABA originating in the hypoxic roots and then transferred to leaves [100–109]. Abscisic acid interferes with stomatal control by impairing guard cell accumulation and/or retention of potassium ions [110] and by causing transient potassium and chloride ion efflux [111]. Markart et al. [112] found that ABA affected the root hydraulic conductivity.

Reduction in leaf conductance (g_s), or increase in diffusive resistance (R_L) to water vapor, directly impacts photosynthesis by concomitantly lowering the rate of carbon dioxide exchange (Figure 17.8). However, because the diffusion coefficient of carbon dioxide in air is only about 60% that of water, assuming all other factors equal, there should be a greater incremental effect of stomatal closure on water vapor transfer than on carbon fixation and photosynthesis. The effect of stomatal closure on C3 plant carbon exchange reduction is greater than on C4 plants because of the steeper concentration gradient to sites of carbon fixation in the C4 substomatal mesophyll [113].

However, explaining the effect of root hypoxia on photosynthesis reduction by only considering the effects on gas transfer into and out of the leaf is an oversimplification. Many biochemical processes within flooded plants are affected by root hypoxia, and the intensity and nature of the aberrations vary with stress scenarios and species as the citations in Table 17.1 bear out. Oosterhuis et al. [60,61] essentially demonstrated this point (Figure 17.8) for soybean. Photosynthesis was depressed to a plateau rate by reduction of stomatal conductance in the presence or absence of flooding, however, the flooded plants had a lower plateau value than the nonflooded plants, indicating the involvement of additional factors. Gardiner and Krauss [114] showed that the photosynthetic light response (Figure 17.9) was reduced by nearly half as the result of flooding of cherrybark oak (*Quercus pagoda*). While stomatal closure may be the most significant mechanism restricting photosynthesis in the early hours of root hypoxia, with prolonged oxygen depravation the rate of photosynthesis declines in response to other inhibitory effects on the photosynthetic process involving changes in carboxylation enzymes and loss of chlorophyll [92,93, 115–117]. Reicosky et al. [118,119] used infrared thermometry to measure increased cotton leaf temperature when plants were flooded. As stomata close, transpirational cooling is reduced. This may also lead to several metabolic stress reactions in addition to de-optimization of photosynthesis if leaf heating
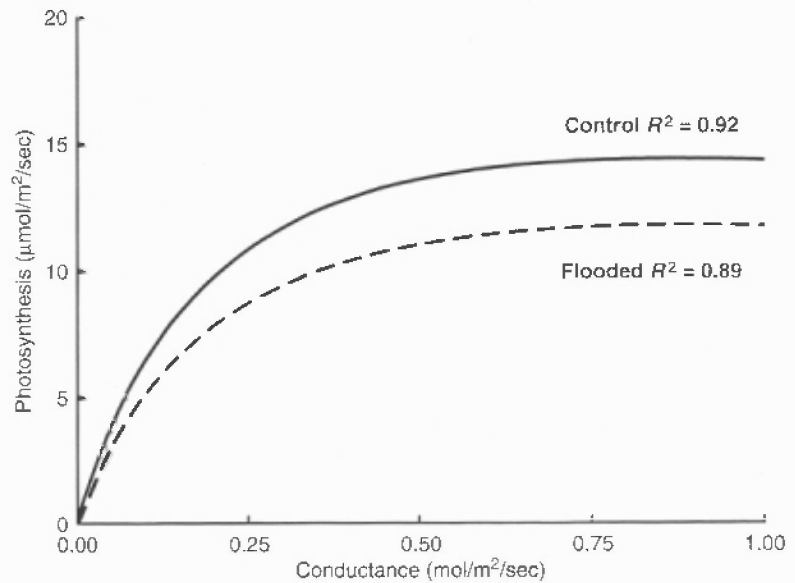
FIGURE 17.8 Difference in the relationship between leaf photosynthetic rate and leaf conductance for flooded vs. nonflooded soybean (From Ref. [9], adapted from Refs. [60,61].)
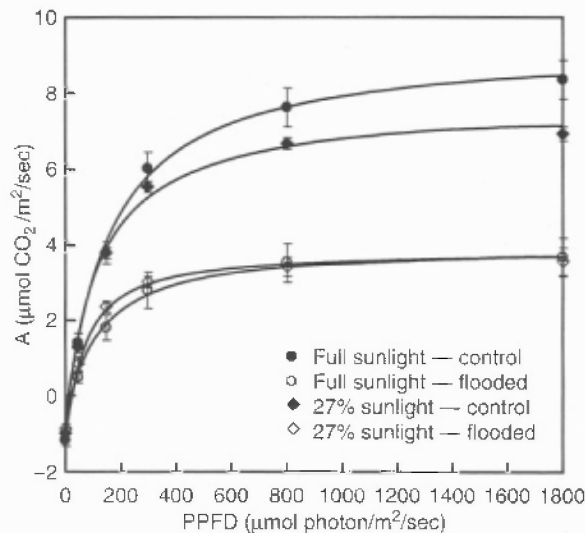
FIGURE 17.9 Net photosynthetic light response of cherrybark oak seedlings grown in full or partial (27%) sunlight and subjected to 30 to 45 days of flooding. Carbon assimilation is reported on a leaf area basis, and each value represents the mean $\forall$ standard error for nine leaves. (From Gardiner ES, Krauss KW. *Tree Physiol.* 2001; 21:1103–1111. With permission.)

causes plants to deviate from their ideal thermal kinetic window [120].

Several other biochemical triggers have been implicated in the closure of stomata of plants exposed to root hypoxia although they have been less intensively researched. These include changes in the nitrogen metabolism of hypoxic plants [121,122], leaf ethylene accumulation [123–127], transport of cytokinin from the roots to the shoot [128], and possibly other as yet unidentified biochemicals acting alone or in concert with other signaling agents [102].

VI.   SUMMARY

The negative effects of flooding and root hypoxia on plant performance has been recognized for centuries and the important role of soil oxygen depravation in triggering the metabolic and physiological changes causing damage have been recognized with increasing clarity for nearly a century. Strong quantitative links between the soil oxygen diffusion rate and leaf conductance to water vapor and other gases have been documented. Flooding effects on plant performance are primarily caused by the sharp reduction in oxygen diffusion to roots, with numerous secondary soil physical and chemical and plant biochemical or pathological effects rapidly ensuing as flooding becomes prolonged. Direct manipulation of soil atmospheres at optimal (nonflooded) soil water contents is a powerful tool for studying plant response with minimal interference of ancillary stress-causing factors. Correlation of stomatal hypoxic response to soil ODR is suggested as the most appropriate way to normalize plant response to the primary environmental stimulus that could facilitate discrimination of species and cultivar sensitivity to hypoxia and offer potential for modeling the response.

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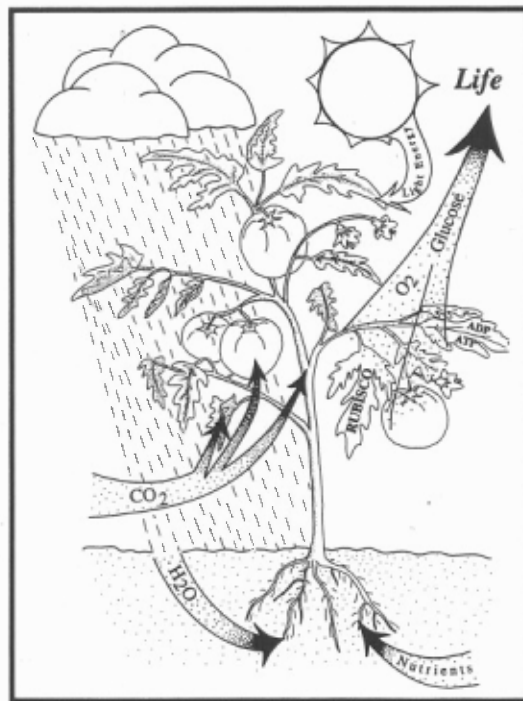106. Wadman-van-Schravendijk H, van Andel OM. Interdependence of growth, water relations and abscisic

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