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Plant injury and adaptation to oxygen deficiency in the root environment: A review

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1. Introduction

Soil compaction during farming operations, particularly under wet conditions, eliminates many of the large diameter 'transmission pores' that serve simultaneously as the major pathways for the drainage of water, the exchange of gases, especially oxygen, between atmosphere and soil, and the unrestricted penetration of roots. Few transmission pores are present in naturally structureless soils dominated by fine sand or silt-sized particles, and the continuity of pores is interrupted by natural or induced pans and surface crusts in a wider range of soil types. When the soil becomes excessively wet, the lack of porosity soon interferes in soil aeration and plant vegetative growth and crop yields are adversely affected[22,32]. This paper reviews (i) the conditions under which the supply of oxygen to plant roots from the soil becomes insufficient for growth and metabolism, (ii) the consequent mechanisms of injury to the vegetative growth of plants that are not adapted to wetland habitats, and (iii) physiological mechanisms by which wetland and non-wetland species acclimatize to a lack of oxygen in the root environment.

2. Oxygen deficiency and the supply of oxygen to roots in soil or solution culture

2.1 Occurrence of anaerobic conditions in field soils

In well-drained land with adequate soil porosity, the flux of oxygen into the soil in response to respiration by roots and soil micro-organisms can be as much as 3.5 to 17 l per day for each m^2 of land surface during the summer in temperate climates, dropping to about one-tenth of this rate during the winter[102]. This flux compares with the volume of O_2 contained in the soil air to a depth of 1 m which would be about 60 l (soil bulk density 1.0 g cm^{-3}, volumetric moisture content, 0.3), sufficient for about 3 days' respiration. Except for plant species that are structurally adapted to allow the internal transfer of oxygen by diffusion from the above-ground parts (see section 5.2 below), oxygen used in root respiration is supplied almost exclusively by the root environment. Although some movement of oxygen into the soil takes place by convection due to fluctuations in air temperature, atmospheric pressure and wind speed, or dissolved in rain[36,43,67], usually these are of minor importance. The principal mechanism is by gaseous diffusion, along gradients of concentration or partial pressure created by the respiratory activity of roots and soil organisms. Well-structured, drained soils provide a sufficiently large cross-sectional area of gas-filled pores that relatively shallow concentration gradients into the bulk soil are adequate for oxygen diffusion, and even at depths of 1–2 m, O_2 partial pressures can be around 0.15 atm, compared with 0.204 atm for water-saturated air.

With flooding, the soil pore space is totally water filled, and gas exchange between soil and atmosphere is virtually eliminated because of the very small diffusivity in water. The oxygenated zone at the soil surface may be confined to a depth of only a few mm. Depending on soil temperature and respiration rates, the rate at which dissolved oxygen in the soil water (about 1.9 l m^{-3} soil) is depleted depends sensitively on the soil temperature and the respiration rate of roots and micro-organisms. With warm temperatures and appreciable amounts of organic matter, or in soil mixed and incubated in the laboratory, depletion may be complete in only hours[112,116]. When temperatures are low and soil respiration is slowed, the concentration of oxygen in the water may decline but slowly. During winter waterlogging of cereals in a clay soil, 13 days elapsed before the concentration of dissolved soil oxygen at 20 cm depth had declined to 0.02 atm. The same change required only 3.5 days in spring[13].

Flooding and the development of anaerobic conditions in the field is usually non-uniform. When the soil water content exceeds field capacity and approaches saturation, an increasing proportion of the micropores in aggregates and peds become water filled. Depending on temperature and its influence on the rate of soil respiration, it can be shown from diffusion theory that the centres of the aggregates 1–2 cm may then become anaerobic but surrounded by a shell of aerobic soil[29,40,96]. Wet soils can thus comprise volumes of anaerobic soil (anaerobic microsites) surrounded by a well-drained macroporous system in which the soil air contains the gaseous products of anaerobic metabolism (*e.g.* N_2O) and, paradoxically, O_2 almost at atmospheric concentration. Alternatively, poor aeration of the soil may arise by surface crusting, or because of a pan beneath the surface. Either effectively seals the deeper soil from the atmosphere, although initially there can be an appreciable air volume trapped beneath the surface water. Less extreme oxygen deficiency can occur where water slowly trickles through the flooded soil so that oxygen concentrations in the rooting zone are much smaller than air saturation, but fully anaerobic conditions are avoided. Thus plants may be subjected in all or part of the rooting zone to anaerobic conditions or to oxygen concentrations ranging from fully air-saturated to anaerobic.

2.2 Oxygen diffusion rates in soil

As long as appreciable concentrations of oxygen remain in the soil water, the respiration of 'unadapted' roots is controlled by the diffusion of oxygen through the soil to their surfaces. Early attempts to estimate minimum oxygen diffusion rates (ODR) through the soil to roots, using cylindrical Pt electrodes[79,109] were severely criticized[88] on the grounds that the fundamental principles concerning the valid use of oxygen electrodes in soil has not been thoroughly established, especially under unsaturated conditions. Particularly damaging was the recognition that reduction of H^+ must have contributed to the current measured in soils at the voltages used by many workers. Thus, many published values of minimum ODRs in soil are unlikely to be fundamentally based.

Such criticism in no way diminishes the importance of diffusion as to a mechanism of oxygen supply in soil containing small concentrations of oxygen. More recently, oxygen flux to Pt microelectrodes in water-saturated soil has been measured, taking care to use voltages at which only the flux of oxygen to the electrode surface could contribute to the measured current[3,14]. In laboratory experiments, oxygen concentration in the soil at 10°C slowly declined, while frequent measurements were made of the extension of the seminal roots of oats (observed through inclined, transparent, container walls)[14]. Oxygen flux to electrodes located in the soil near the extending roots was also monitored. The time at which the rate of root elongation first declined was that at which oxygen flux to the electrode diminished to 56 ng cm^{-2} min^{-1}, a flux that calculations suggest would be just sufficient to maintain the oxygen consumption rate of the root apex. When oxygen flux to the Pt electrode was effectively zero, root extension ceased[14]. Such observations suggest that in unstirred, water-saturated media the electrode method can, with appropriate safeguards, give a reliable estimate of the maximal potential supply of oxygen to a root surface.

2.3 Models of oxygen diffusion to and in roots

Quantitative estimation of the conditions under which oxygen diffusion through the soil to the root surface would be likely to limit respiration were developed by Lemon[78] and by Luxmoore *et al.*[84–87]. The latter model also took account of the longitudinal diffusion component within intercellular spaces, radial leakage, and respiratory oxygen consumption within the root. Unfortunately Luxmoore *et al.* assumed that the latter relation was adequately described by their measured rates of oxygen uptake by root segments in a respirometer, in which half-maximal oxygen uptake occurred at 0.08 atm (maize) and 0.16 atm (rice) oxygen partial pressure. The data obtained from their calculations was called in question by Armstrong and Gaynard[2] who pointed out that respirometer oxygen concentrations refer to the external gas phase and such concentrations are greatly in excess of the critical oxygen pressures (see below) defined with respect to intercellular oxygen concentrations in their own investigations. It would be interesting to re-examine the model of Luxmoore *et al.*[84] using revised boundary conditions.

More recently, Armstrong and co-workers[4] have used an electrical analogue to simulate oxygen diffusion and consumption in the plant–soil system. Oxygen concentrations reaching cells in the meristematic zone of the root, a critical consideration for root growth, are reduced by: the length of the diffusion path from the shoot; by fast radial leakage from the root to the surrounding medium; by a small gas-filled porosity; and by rapid respiration of cells along the diffusion path. On the assumption that root growth (cell division and expansion) would cease when the partial pressure of oxygen bathing the meristematic cells declined to 0.02 atm, Armstrong[1] calculated the maximum length to which roots would be expected to extend in anaerobic media. For roots of the dimension of wheat, with an internal porosity of 15% and slow respiration, maximal extension would be about 17 cm (Armstrong[1], Fig 17F). This compares well with the maximum length of wheat aerenchymatous roots observed in anaerobic soil (20 cm)[112] and anaerobic solution culture (12 cm)[114].

3. Oxygen requirements of roots in solution culture

The oxygen concentration in the outer solution at which oxygen consumption rates begin to be slowed by oxygen shortage is defined as the critical oxygen pressure (COP)[9,23]. Knowledge of the COP for different species was at one time judged important because it was anticipated that roots of wetland and dryland species would display contrasting values. Additionally, by comparing the COP with the oxygen concentration in the rooting medium it seemed that a simple means was available for assessing the oxygen supply to roots that was equally relevant to studies in soil and in solution culture.

Oxygen consumption rates decrease hyperbolically as the oxygen concentration decreases below the COP. With excised roots, the COP is appreciably greater

Table 1. Critical oxygen pressures for respiration of onion (*Allium cepa*) root segments as a function of temperature*

	Root segment: distance from tip (mm)		
Temperature (°C)	0–5	5–10	10–15
15	0.15	0.10	0.10
20	0.20	0.15	0.15
30	0.50	0.20	0.10
35	0.50	0.40	0.20

* Values in the Table show the oxygen partial pressure in the manometer flask in atmospheres (air = 0.21). Data from Berry and Norris[9].

for the apical 0–5 mm segment which has the highest oxygen uptake rate[9]. As the temperature is raised from 15°C to 35°C (Table 1), the COP for any segment increases. At 35°C maximal respiration rates are not attained until the oxygen partial pressure equals or exceeds that in air. At partial pressures below the COP, the respiratory quotient (volume CO_2 emitted/volume O_2 consumed) becomes progressively greater, suggesting that extra CO_2 is produced by anaerobic respiration in at least part of the tissue. Berry and Norris[9] concluded that when the oxygen concentration falls below the COP, the rate of oxygen consumption is limited by diffusion across the tissue. Thus, an outer 'sleeve' of fully aerobic tissue may surround a central 'core' of anaerobic cells. Although the presence of an 'anaerobic core' has yet to be demonstrated directly, strong support for the notion is given by the sharp rise in the production of ethanol (or alcohol dehydrogenase activity) together with the appearance of 'anaerobic polypeptides' (stress proteins characteristic of anoxic cells) in wheat roots when the oxygen partial pressure is reduced to 0.10 atm or less[11].

The partial pressures of oxygen at which various root functions that are dependent on concomitant respiration begin to be restricted show a wide range in different investigations. In vigorously stirred solution, root extension rates in tobacco and soybean at oxygen concentrations as low as 0.02–0.03 atm were almost as rapid as in air-bubbled solution[46]. Uptake of ions[46] and water[124] were also nearly maximal at these low oxygen concentrations. By contrast, root extension observed by other workers[11,12,83,117] was slowed at concentrations about half that in air, *i.e.* 0.1 atm. It is difficult to know whether such a range of oxygen partial pressures is simply a consequence of the efficiency of stirring of the nutrient solution. Although measurement of the oxygen concentration in the outer solution is widely accepted as a relative measure of the supply of oxygen to the tissues, it becomes of doubtful value in comparing different experimental conditions or species with precision. Unstirred layers of solution at the root surface will impede gaseous diffusion and affect the concentration gradient, especially at low oxygen concentrations. In some species, appreciable wall resistance is offered to gaseous diffusion, so that the internal concentration can be much lower than in the bulk solution. An unknown contribution to oxygen supply may originate by internal diffusion through intercellular spaces connecting with the shoot. Furthermore, only a fraction of the oxygen consumption may be associated with oxidative phosphorylation, and this could vary with the environment and stage of development of the root tissue. In conclusion, it is difficult to make a general prediction concerning the oxygen requirement of roots based on the external concentration of oxygen.

In an attempt to overcome the above uncertainties and define the critical oxygen pressure with greater precision, Armstrong and co-workers[2,121,122] used cylindrical Pt electrodes placed around the root tip to obtain estimates of the oxygen concentration in the intercellular spaces and so deduce the COP at the cellular or tissue level. They found that for two wetland species, rice and cotton grass (*Eriophorum angustifolium*), respiration in the root cortex would be maintained by oxygen concentrations as small as 0.001 atm, while the more tightly packed cells in the apical meristem and stele might require 0.02 to 0.026 atm oxygen concentration in the internal gases. These values are very similar to estimates[121,122] (0.002 to 0.0207 atm) of the internal COP for roots of pea (*Pisum sativum*), a species that is particularly susceptible to flooding[21,49], suggesting that the poor tolerance of the latter cannot be attributed to a greater oxygen requirement for respiration.

Although the internal COP in roots is much smaller than the oxygen concentration in air-saturated water, it is still appreciably greater than the concentration at which the binding of oxygen to cytochrome oxidase within mitochondria would be virtually saturated (K_m about 0.1 μM[15], compared with the concentration of dissolved oxygen in water at 15°C and 0.206 atm partial pressure which is 314 μM). This suggests that diffusion of dissolved oxygen from the intercellular spaces across the cell to mitochondria adds a further appreciable resistance to the overall pathway of oxygen diffusing from the outer solution.

4. Mechanisms of plant injury induced by oxygen deficiency

4.1 Injury to roots

Understanding of the mechanisms by which the growth and metabolism of flood sensitive species are affected when the soil becomes oxygen deficient has been greatly influenced by the early work of P. J. Kramer[69]. Kramer demonstrated that factors damaging to the plant may originate in the soil, or in the plant

Table 2. Possible mechanisms of injury to plant roots in flooded soil

O_2-deficiency	*Toxic substances*	*Toxic substances*
limits aerobic respiration. Lack of ATP to drive root metabolism. Lack of respiratory substrates	accumulate in anaerobic soil, *e.g.* organic acids, NO_2^-, Mn^{2+}, Fe^{2+}, H_2S	produced by anaerobic metabolism in roots, *e.g.* acetaldehyde, ethanol

itself, and that the root or shoot or both may be susceptible to injury. Although lack of oxygen is undoubtedly the trigger for changes in the metabolism of roots and soil micro-organisms, oxygen deficiency may not always be the immediate cause of injury to the root (Table 2). Ionic species with a greatly increased solubility in the reducing soil environment, or intermediates in microbial carbon metabolism, can sometimes accumulate to concentrations that can be shown to be damaging to plants in solution culture (reviewed in Refs.[30,32]). Anaerobic respiration of roots gives rise to end products that are potentially harmful when accumulated in large concentrations. However, the view[27] that cell death in the roots of flood sensitive species under anaerobic conditions is invariably caused by an accumulation of ethanol arising from fermentation is now in doubt. Roots or isolated protoplasts are not especially sensitive to exposure even to ethanol concentrations one or more orders of magnitude greater than those encountered within flooded plants[54]. The alternative view is that anaerobic respiration produces insufficient ATP for growth and cell maintenance. The ability of anoxia-intolerant roots to survive continuously anaerobic conditions is of short duration, ranging from 0.5–3 h for cotton tap root (*Gossypium hirsutum*)[47] to 96–120 h for rice seminal root[12]. But root survival of anoxia can be extended by exogenous supplies of carbohydrate[122] suggesting that cells soon use up their supplies of easily-respired substrates, while further translocation of substrates from shoot to root are presumably curtailed.

Such conclusions concerning the shortage of respirable substrates are supported by observation of changes in the adenylate energy charge (AEC) in maize root tips[103]. The AEC, given by ([ATP]+0.5 [ADP])/([ATP]+ADP]+[AMP]) is a measure of the energy status of the cell, and the effectiveness of respiration in maintaining it[5,94,95]. An AEC value of 1.0 would indicate that all the adenine nucleotides in the pool maintained by adenylate kinase had been converted to ATP. Healthy vegetative cells tend to stabilize the AEC in the range 0.8 to 0.95. In freshly excised root tips of maize, Saglio *et al.*[103] found that the AEC in air (0.9) declined within 30 minutes after transfer to a nitrogen atmosphere to values of 0.6. If the excised roots were allowed to age in air so that their soluble sugars were depleted by respiration, the AEC declined still further to 0.15 after 30 minutes' anoxia. However, addition of glucose caused a partial restoration of the energy charge, to 0.6.

4.2 Injury to shoots

Mechanisms of flooding response and injury in the aerial parts of the plant that are not submerged differ fundamentally from those in roots in that they take place in tissues that are not directly subjected to oxygen shortage. In broad terms, interference in root growth and function in the flooded soil must lead either to an insufficient supply to the shoots of essential substances (water, phytohormones, nutrient ions) or to the abnormal supply of substances, including toxins, originating in the anaerobic soil or in the roots themselves (Fig. 1). The possible mechanisms and at least some of their inter-relationships are summarized in Fig. 1: the bottom line gives the symptom ultimately detectable in the shoot. It should be emphasized that not all of the above mechanisms necessarily take place in the same species, or simultaneously, and information concerning inter-relationships is incomplete.

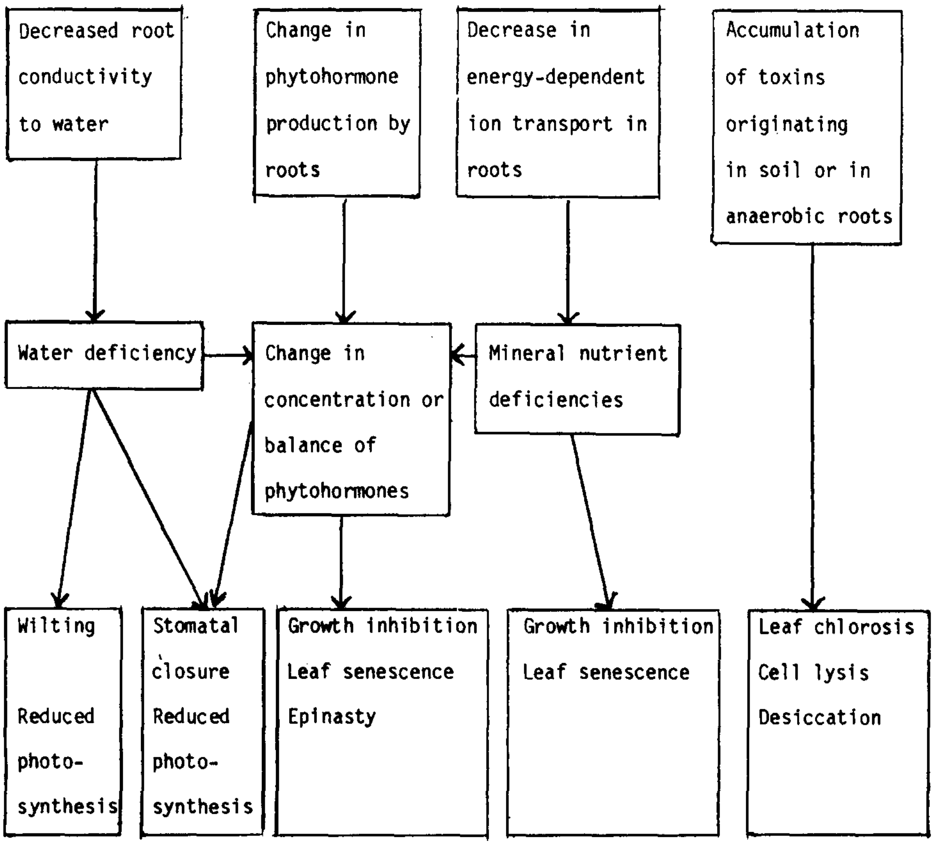

Fig. 1. Possible mechanism of flooding response and injury to shoots

In terms of plant water relations, flooding causes a decrease in the exudation rate of detopped roots[69], probably as a direct consequence of a transient decrease in cell membrane permeability to the radial passage of water under anoxia[16,90,92]. The conditions under which this change in root conductivity affects the water relations of the shoot is uncertain and may vary greatly between species. In some, there appears to be a decline in leaf water potential and wilting occurs[69,70]. In others, stomatal closure has been shown to occur shortly after the onset of flooding or under anoxia[44,53,54,106] and no wilting is observed. Leaf water potential in flooded plants may then become greater (less negative) than in unstressed controls[16,53]. An additional factor may also contribute to the maintenance of the leaf water status. Following a period of high resistance to water movement, roots can become much more conducting than controls, presumably when membrane degradation accompanies cell death[16,69]. The consequences for the leaves of these marked reversals of root resistance to water uptake within the period of a day or so are not well understood. A rapid restoration of the water supply to the shoot may explain why wheat plants in anaerobic solution culture failed to show any decline in net carbon fixation per unit leaf area, or in transpiration, during the initial 8 days of treatment, presumably because stomata remained open[114]. However, where stomatal closure induced by flooding occurs, photosynthesis is clearly slowed, as in *Populus deltoides*[98]. Wilting, and associated stress of the photosynthetic apparatus would also be expected to reduce the rate of photosynthesis.

Although it is well recognized that roots are sources for phytohormones, their unambiguous influence on growth and metabolism of the shoots remains to be demonstrated. Thus, the supply of cytokinins and gibberellins from roots to shoots is blocked by flooding[19,99], but the link with visible symptoms of injury or with metabolic events in the shoot is tenuous: general inhibition of growth, or premature leaf senescence have been attributed to reduction of phytohormone supplies but the symptoms are not sufficiently precise to permit a firm conclusion since they might be triggered by other factors[33]. Spraying leaves with synthetic cytokinins[97] or with mixtures of cytokinins and gibberellins[51,104] gave only a partial restoration of growth and leaf chlorophyll in the shoots of flooded plants. The difficulty of maintaining physiologically normal supplies is an area of uncertainty: sprays of cytokinins caused abnormal wilting of leaves presumably by maintaining stomatal opening, so that it is clear that the spray has done more than simply restore the supply which would have been derived from the root.

Among the phytohormone responses, those related to ethylene have been most thoroughly characterized. Leaf epinasty in tomato is stimulated by flooding the root system, or by root anoxia[50,53]. An ethylene precursor (ACC 1-aminocyclopropane-1-carboxylic acid), is synthesized in the roots at an accelerated rate under conditions of oxygen shortage[17]. The movement of ACC from the roots to the well aerated aerial tissues allows conversion to ethylene through an oxygen-requiring reaction in the stem and leaves. It has also been suggested[52] that increased concentrations of ethylene in the shoots might cause a non-specific growth inhibition, depressing leaf extension and the associated requirements for water and inorganic ions at a time when the function of the root is greatly impaired. Abscisic acid (ABA) in leaves shows an appreciable increase when oxygen is excluded from around the roots[44]. Extra ABA may explain, at least for some species, the promotion by flooding of stomatal closure and slower growth, but the time course of ABA increases have yet to be accurately compared with physiological symptoms in the shoots. Furthermore, the mechanism causing the release of ABA in leaves remains obscure. One possibility is that it is caused by a brief water stress in leaves, reflecting the early, transient decrease in root conductivity referred to above.

With flooding, concentrations of nitrogen, phosphorus and potassium in the shoots of soil grown plants decline[72,80–82]. In experiments with barley and wheat we have found that this effect is not necessarily the consequence of leaching the soil nutrient, or denitrification (although these may contribute under field conditions), but rather, the result of the inhibition of ion uptake while the shoot continues to photosynthesize and gain dry matter[34,112]. Comparable depressions of nutrient ion accumulation by shoots can be brought about in deoxygenated solution culture[114] or in soil perfused with oxygen-depleted air[35]. If we concern ourselves with the mineral nutrition of the plant alone, then the failure of the roots to supply the shoots with inorganic ions somehow leads to premature senescence of the older, lower leaves. Translocation of nutrients (N, P and K) out of the senescencing leaves to the younger emerging ones, is detectable within 2–4 days, but the process of reallocation within the shoot is insufficient to maintain a favourable concentration in the younger leaves, which develop only slowly[34,113]. With barley we found that a similar promotion of senescence in older leaves could be brought about under well-aerated conditions in solution simply by depriving the plants of a source of nitrogen (see Ref.[32] for a summary).

Support for the view that interference in the normal mineral nutrition of the plant contributes to decreased growth during flooding or anoxia comes from experiments in which attempts were made to maintain the nutrient status of the shoot. Foliar feeding urea as a relatively non-toxic nitrogen source to the leaves of wheat delayed leaf senescence but failed to support shoot growth during flooding[113]. When a single seminal root was supplied with nutrient solution under well-aerated conditions, while the remainder of the root system was kept in *anaerobic* nutrient solution, there was no leaf senescence or growth retardation[115]. Furthermore, young wheat plants raised under conditions that encouraged a high nitrogen status *before* an anaerobic treatment to the roots were clearly less susceptible to injury and growth inhibition than nutrient-impoverished plants[115]. A relatively high concentration of nutrients in the rooting medium *during* the anaerobic treatment was also of advantage to the shoot[115], probably because of the greater quantities of ions leaking across the root to the xylem[114]. Taken together, the evidence strongly suggests that the mineral nutrition of the shoot is profoundly modified by flooding, although it is possible that the supply of inorganic ions exerts part of its effect through the requirement for phytohormones[115].

By contrast to the major nutrient ions, sodium concentration in the shoots of cereals becomes *greater* during flooding of the soil[80,81], or when roots are made anoxic in nutrient solution[46]. Such increases in sodium content are known to give rise to economically important depressions of crop growth and yield[39]. In salt sensitive species and varieties, sodium ions usually are prevented from entering the shoot in damaging amounts by the operation of an outwardly directed sodium pump[57,58] and by the resorption of sodium as it passes up the xylem in the transpiration stream by the xylem parenchyma cells that border the xylem[71,105,125]. It seems reasonable to anticipate that the mechanisms of sodium exclusion would depend on aerobic respiration and the active transport of ions outwards. However, the incidence of excessive entry of sodium to the shoot and poor root aeration have not been systematically studied. During irrigation when soil temperatures are high, oxygen is rapidly depleted from the soil solution[48]. The effects of a short period of oxygen deficiency could be much more severe where the irrigation water contains appreciable salt concentration.

4.3 Temperature dependence

The rapidity with which waterlogging sensitive plants succumb is greatly dependent on the ambient temperature[8,41,100,107,111,118]. Part of the explanation of this effect is undoubtedly the rate at which dissolved oxygen is depleted from the soil water. In temperate climates, it can take as much as 13 days' waterlogging for the soil oxygen in the field at 20 cm depth to become depleted in the winter compared with 3.5 days in spring[13]. However, part of the response to temperature is controlled by the plant. Laboratory experiments with controlled conditions of oxygen supply (which eliminate any possibility of a variable, slow decline in oxygen concentration) show that plant damage still becomes detectable more quickly at higher temperatures[81,119]. In experiments in which plants were grown in well aerated soil at 14°C and then subjected to different root temperatures, flooding the soil led to complete oxygen depletion in 12 to 48 h (temperature range 18°C to 6°C)[116]. However, despite the relatively rapid onset of anaerobic conditions at all temperatures, after 14 days' waterlogging all symptoms of waterlogging damage (leaf senescence; slower extension of leaves, slower dry matter accumulation by roots and shoots) were more advanced at 18°C compared with aerated controls at the same temperature. But when plants were grown throughout at different root temperatures and then flooded and sampled at the same growth stage, injury symptoms developed to a similar extent despite the temperature differences. Thus, the apparently greater tolerance of wheat to flooding at low temperatures may in part be a consequence of a smaller relative growth rate.

5. Metabolic and structural adaptations to oxygen deficiency

5.1 Metabolic adaptations

Anoxia-intolerant plant species survive oxygen-free conditions for periods ranging from hours to days, but eventually degenerate. By contrast, anoxia-tolerant plants or organs survive much more extended periods. Seedlings of the wetland grasses, *Deschampsia aespitosa* and *Molinia caerula* were fully viable after 8 days in an anaerobic workbench in which the environment was kept totally oxygen-free[7]. In further observations with plants kept in an anaerobic environment[28], the rhizomes, buds and roots of a number of wetland species that over-winter in anaerobic mud survived for an indefinite period of 2 months or more for *Scirpus maritima* and for 1 month or more for *Schoenoplectus lacustris*, *S. tabernaemontani*, *Typha angustifolia*, *Phragmites australis* and *Iris pseudacorus*. The possibility that the submerged organs of flood-tolerant species might possess an alternative respiratory metabolism to that of flood-susceptible species has long been a subject of interest. A generalized metabolic theory of flooding tolerance was developed by Crawford and co-workers[25–27,38,89]. In this, the success of flood-tolerant species was ascribed to the ability to continue to respire (anaerobically) by the Embden–Meyerhof–Parnas glycolytic pathway and regenerate NAD from the NADH produced during glycolysis, so as to maintain the operation of the pathway. Avoiding the synthesis of potentially injurious ethanol during the regeneration of NADH was thought to be of paramount importance. There was evidence that flood-tolerant species converted phosphoenol pyruvate (PEP) to oxaloacetate and thence to malate, presumably a less harmful end-product than ethanol. By contrast, flood-susceptible species were found to respire rapidly with generation of ethanol in concentrations presumed to be toxic to root cells. Other end products, that may provide a non-toxic means for regenerating NAD, have been identified as glycerol, shikimate, lactate and the amino acids, alanine and glutamate[27].

A major difficulty over acceptance of the metabolic theory has been to understand the means by which the energy requirements of the anaerobic cells could be maintained: respiration of a hexose sugar to the level of malate gives no net yield of ATP, and if starch is the respiratory substrate, only one mol of ATP would be derived for each hexose moiety. Furthermore, in complete contrast to Crawford's hypothesis, a number of flood-tolerant species including herbacious monocotyledons[6,12,91,101,123] and woody dicotyledons[45,59,60,65,66] clearly derive their energy from the synthesis of ethanol. This would generate 2 mol ATP per mol of hexose respired. Ethanol toxicity is avoided by 'its removal either in the transpiration stream[37,54], or to the rooting medium[12,45]. The significance of the metabolic theory must therefore remain in doubt until tested further.

The possibility that flood-tolerant and -susceptible species might differ in the affinity of their terminal oxidases for oxygen has been explored by Lambers and colleagues using *Senecio* species[73–76]. Because the operation of the alternative pathway gives rise to much less ATP synthesis than the conventional cytochrome pathway[77,108], the extent to which the alternative pathway is engaged *in vivo* could be important in roots in which respiration and ATP synthesis are restricted by lack of oxygen. However, susceptibility to flooding was found not to be related to a greater activity of the alternative (cyanide resistant) pathway, since this contributed to about the same extent to total respiration in *S. aquaticus* (flood tolerant) and *S. jacobea* (flood susceptible)[73]. In pea, which is highly flood susceptible, the alternative pathway was found not to be operative in the roots[121] so that the majority of the oxygen consumption was presumably associated with oxidative phosphorylation via the cytochrome pathway. By contrast, in flood-tolerant *Senecio aquaticus* with the roots in nitrogen-bubbled solution, the consumption of oxygen (obtained by diffusion from the shoot) was estimated to fall in half the rate in air-bubbled solution, but oxidative phosphorylation was unimpaired[76]. This would be expected if only the oxidases that contribute nothing to oxidative phosphorylation become inhibited at oxygen concentrations that are just below the critical oxygen pressure because of their low affinity for oxygen compared with the unknown terminal oxidase of the alternative pathway and with cytochrome oxidase.

In conclusion, there is no evidence to suggest that flood-susceptible species are less efficient in their utilization of oxygen in respiration than are flood-tolerant species. The mechanism by which anoxia-tolerant organs survive[7], or in the case of some rhizomes, exhibit leaf extension[28], remains to be determined. Recently attention has turned to the possibility that the composition of membrane lipids (especially in relation to the synthesis of unsaturated fatty acids which is dependent on molecular oxygen[110]) could play a key role in anoxia tolerance[24,42,120].

5.2 Structural adaptations

The ability of herbaceous wetland species to tolerate flooding is frequently associated with the production of numerous adventitious roots that emerge from the base of the shoot[1,63]. The roots develop gas-filled spaces (aerenchyma) which interconnect longitudinally and join up with the gas spaces of the stem base[18]. There is thus a pathway of low resistance for the diffusion of oxygen from the air. It is difficult to prove that plant survival is dependent on the formation of such roots, since it could be argued that species or individuals that are capable of survival subsequently develop aerenchymatous roots. However, if it can be shown that such roots are functional, and replace the initial non-aerenchymatous roots that had grown before flooding, it is reasonable to suppose that plant 'fitness' to the environment is improved. The response is not restricted to herbaceous plants. In some temperate and tropical forest tree species tolerant of high watertables, gas spaces form in the pith and help conduct oxygen into the roots and oxidize the rhizosphere[45,65,66,93].

An ability to form adventitious, aerenchymatous roots is also evident in a wide range of crop species that are not intentionally grown on wet sites, although the numbers of such roots that are initiated from the stem base, and the fraction of their volume that becomes gas-filled, are appreciably smaller than in wetland species[63,64,112,114]. These features, combined with delay in their initiation and their low extension rate probably explain the inability of the adventitious roots to totally compensate for the loss of the earlier roots. By analogy with their occurrence in wetland species, it is reasonable to assume[56,69] that the aerenchymatous root system in non-wetland species partially offsets the degeneration of the initial non-aerenchymatous roots during flooding. It is clear that the aerenchymatous root structure readily permits the transport of ions to the xylem and their translocation to the shoot (reviewed in Ref.[32]), despite the destruction of much of the root cortex that accompanies gas-space formation.

The mechanism controlling aerenchyma formation has at present only been studied in maize. Under conditions of oxygen shortage (hypoxia) but not anoxia, cell lysis and gas space formation take place specifically in the cortex in response to an acceleration of ethylene biosynthesis and increased internal concentrations of the gas[20,31,68]. Aerenchyma readily develops in roots when they are fully aerobic while supplied with exogenous ethylene at low concentration ($1\ \mu l\ l^{-1}$ or less) but this response can be blocked in the presence of low, non-toxic concentrations of Ag^+ which is known to inhibit ethylene action in plants. Silver ions likewise prevent the formation of aerenchyma in roots subjected to oxygen shortage[31]. It would be interesting to know more about the processes by which an oxygen shortage in roots stimulates their ethylene biosynthesis, recognizing that the formation of the intermediate S-adenosylmethionine from methionine requires ATP, and the conversion of the precursor ACC to ethylene requires molecular oxygen[17].

Although the occurrence of aerenchyma in roots is an important acclimatic feature, it is not invariably associated with an ability to survive wetland conditions. Of the 5 flood-tolerant tropical trees studied by Joly[61,62], two did not develop roots of increased porosity and only one developed hypertrophied lenticels at the base of the shoot (a response to flooding which can improve gas exchange and hence root aeration).

6. Conclusions

The response of plants to flooding indicates that a variety of strategies have evolved that are conducive to survival. Some species and organs have developed an effective means for continuing glycolysis and fermentation so that the energy requirement of cells can be at least partially maintained, while the ethanol produced in fermentation is lost by transpiration or by leakage to the root environment. The coleoptiles of rice[6,12,59,91] and of barnyard grass[101] seem to owe their anoxia tolerance to this strategy. The energy metabolism and respiratory pathways of carbon in anoxia-tolerant rhizomatous wetland species has not yet been examined. However, the ability to avoid rapid mobilization of carbohydrates in the rhizome[28] suggests that energy may be derived from a slow, carefully controlled alcoholic fermentation. Once the coleoptile or developing shoot breaks the water surface, further growth of the submerged organs clearly depends on internal transport of oxygen through highly porous shoot, stem and root, thereby avoiding further oxygen deficiency.

The variety of survival strategies used by tropical tree species has been well described by Hook and Scholtens[45] and Joly and Crawford[62]. Both groups establish that flooding tolerance is not associated invariably with any single characteristic. Metabolic, anatomical and morphological features of roots and shoots combine to allow various degrees of anoxia tolerance or anoxia avoidance. In the future it may prove possible to incorporate some of these favourable characteristics into flood-susceptible crop plants to improve their resistance to temporary flooding.

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