

Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots

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ABSTRACT

Internal transport of gases is crucial for vascular plants inhabiting aquatic, wetland or flood-prone environments. Diffusivity of gases in water is approximately 10 000 times slower than in air; thus direct exchange of gases between submerged tissues and the environment is strongly impeded. Aerenchyma provides a low-resistance internal pathway for gas transport between shoot and root extremities. By this pathway, O₂ is supplied to the roots and rhizosphere, while CO₂, ethylene, and methane move from the soil to the shoots and atmosphere. Diffusion is the mechanism by which gases move within roots of all plant species, but significant pressurized through-flow occurs in stems and rhizomes of several emergent and floating-leaved wetland plants. Through-flows can raise O₂ concentrations in the rhizomes close to ambient levels. In general, rates of flow are determined by plant characteristics such as capacity to generate positive pressures in shoot tissues, and resistance to flow in the aerenchyma, as well as environmental conditions affecting leaf-to-air gradients in humidity and temperature. O₂ diffusion in roots is influenced by anatomical, morphological and physiological characteristics, and environmental conditions. Roots of many (but not all) wetland species contain large volumes of aerenchyma (e.g. root porosity can reach 55%), while a barrier impermeable to radial O₂ loss (ROL) often occurs in basal zones. These traits act synergistically to enhance the amount of O₂ diffusing to the root apex and enable the development of an aerobic rhizosphere around the root tip, which enhances root penetration into anaerobic substrates. The barrier to ROL in roots of some species is induced by growth in stagnant conditions, whereas it is constitutive in others. An inducible change in the resistance to O₂ across the hypodermis/exodermis is hypothesized to be of adaptive significance to plants inhabiting transiently waterlogged soils. Knowledge on the anatomical basis of the barrier to ROL in various species is scant. Nevertheless, it has been suggested that the barrier may also impede influx of: (i) soil-derived gases, such as CO₂, methane, and ethylene; (ii) potentially toxic substances (e.g. reduced metal ions) often present in waterlogged soils; and (iii) nutrients and water. Lateral roots, that remain permeable to O₂, may be the

main surface for exchange of substances between the roots and rhizosphere in wetland species. Further work is required to determine whether diversity in structure and function in roots of wetland species can be related to various niche habitats.

Key-words: aerenchyma; carbon-dioxide; diffusion; ethylene; pressurized flow; methane; oxygen; plant aeration; radial oxygen loss; roots; wetland plants.

INTRODUCTION

Internal transport of gases is crucial for vascular plants inhabiting aquatic, wetland, or flood-prone environments. Direct exchange of O₂ between submerged tissues and the environment is strongly impeded; O₂ diffusivity in water is approximately 10 000 times slower than in air. Transport of O₂, and other gases, within plants is enhanced by tissues high in porosity (gas volume/tissue volume) (Armstrong 1979). Porosity in plant tissues results from the intercellular gas-filled spaces formed as a constitutive part of development (Sifton 1945, 1957; Roland 1978; Jeffree, Dale & Fry 1986; Raven 1996), and it can be further enhanced by formation of aerenchyma (Armstrong 1979). Depending on the species and environmental conditions, aerenchyma form in newly emerged adventitious roots (Drew, Jackson & Giffard 1979; Trought & Drew 1980; Jackson & Drew 1984), young seminal roots (Konings 1982; Thomson *et al.* 1990), the shoot base (Jackson 1989), and stems, petioles, and rhizomes (Arber 1920; Laing 1940; Sculthorpe 1967; Brix, Sorrell & Orr 1992). Aerenchyma in roots usually forms in the cortex (Armstrong 1979), and in rhizomes and stems the aerenchyma (often termed lacunae) occur in the cortex and also in the pith cavity (Armstrong J & Armstrong 1988).

Evidence supporting the importance of internal aeration for plant growth in waterlogged soils and flood-prone environments is as follows. (i) Mathematical models indicate the dependence of root penetration into anaerobic substrates on internal O₂ diffusion (Armstrong 1979; Armstrong & Beckett 1987), and highlight differences between species in internal aeration capacity that may determine relative waterlogging tolerance (Sorrell *et al.* 2000). (ii) Species with higher root porosity tend to form deeper roots and are more tolerant of soil waterlogging (Armstrong 1979; Justin & Armstrong 1987; Laan *et al.* 1989). For exam-

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ple, lateral roots of *Rumex thyrsiflorus* with porosity of ~5% penetrated at most 100 mm, whereas those of *Rumex maritimus* with porosity of ~30% penetrated 400 mm, when grown in waterlogged soil (Laan *et al.* 1989). (iii) Adenylate energy charge in submerged root tissues was much better maintained when there was internal aeration via the aerenchyma (Drew, Saglio & Pradet 1985; Große & Bauch 1991). (iv) Die-back of *Phragmites australis* stands in wetlands of northern Europe has been linked to factors (cutting, insect damage, or callus formation in aerenchyma) that impede internal aeration (Armstrong J, Afreen-Zobayed & Armstrong 1996a; Armstrong J *et al.* 1996b; Armstrong J & Armstrong 2001a). Nevertheless, other traits also contribute to plant adaptation to wetland environments. For example: (i) metabolic processes involved with survival during, and recovery from, anoxia (Drew 1997); (ii) submergence-induced extension of shoot organs (Ridge 1987; Voesenek & Blom 1989; Sauter 2000) so that plant contact with the atmosphere is maintained (or re-established) as floodwaters rise, enabling continued exchange of gases; and (iii) life history traits, such as timing of seed dispersal (Blom 1999).

Understanding the processes involved in plant aeration is of importance for management of wetlands (Rolletschek *et al.* 2000), design of constructed wetlands for waste water treatments (Armstrong J, Armstrong & Beckett 1992), and to improve waterlogging tolerance in crops (Thomson *et al.* 1992; Taeb, Koebner & Forster 1993; Ray, Kindiger & Sinclair 1999; McDonald, Galwey & Colmer 2001a). The present report summarizes the roles of diffusion and pressurized through-flow of gases in plant aeration, and identifies areas requiring clarification. The physiological and ecological significance of exchange of gases between roots and waterlogged soils is also considered. For example, whereas roots receive O₂ from the shoots and lose some to the soil, CO₂, ethylene, and methane from the waterlogged soil enters the roots and is vented to the shoots. Moreover, the functional significance of a barrier to radial O₂ loss (ROL) for roots in waterlogged soils is highlighted.

AERENCHYMA: A PATHWAY FOR LONG DISTANCE TRANSPORT OF GASES IN PLANTS

Intercellular gas-filled spaces are present throughout almost the entire body of plants, the exceptions being meristems and vascular bundles (Sifton 1945, 1957; Armstrong 1979; Raven 1996). These constitutive spaces are formed by schizogenous cell separation during tissue and organ development (e.g. Roland 1978; Jeffree *et al.* 1986). Intercellular gas spaces are particularly well developed in the spongy leaf parenchyma (Jeffree *et al.* 1986), and also in other tissues high in parenchyma (e.g. the cortex of stems and roots) (Sifton 1945). The gas space network is interconnected between shoots and roots (Evans & Ebert 1960; Greenwood 1967; Healy & Armstrong 1972; Armstrong 1979), and it may have been under selection pressure in early land

plants embedded in frequently waterlogged substrates (Raven 1977).

Porosity resulting from constitutive intercellular gas spaces can differ markedly among species, depending on the pattern of cell arrangements. Assuming perfectly spherical cells in point contact with each neighbouring cell, hexagonal packing gives a porosity of approximately 9% whereas cuboidal packing gives 21% (Yamasaki 1952; Justin & Armstrong 1987). Cells in plant tissues, however, are not spherical and have considerably more 'contact' with neighbours, so that root porosity is smaller than described above. The relative differences in porosity between tissues with these two types of cell arrangements, however, become larger as 'contact' between adjacent cells increases (Justin & Armstrong 1987). For example, porosity was ~9% at 10–20 mm behind the apex in rice adventitious roots with cuboidal packing in the cortex (Armstrong 1971), and can be as low as 1% in roots with hexagonal cell arrangements (Justin & Armstrong 1987). Cuboidal arrangement of cortical cells occurs in the roots of many (although not all) wetland species, but can also occur in some dryland species (Justin & Armstrong 1987; Gibberd *et al.* 2001; McDonald, Galwey & Colmer 2002). The consequence for internal O₂ diffusion of having either packing configuration in the mid-cortex, when extensive aerenchyma is also present (e.g. root porosity may reach 55% in some species), remains to be determined. The aerenchyma, however, usually terminates a few centimetres behind the tip in roots of wetland (e.g. rice, Armstrong 1971) and non-wetland (e.g. sunflower, Kawase & Whitmoyer 1980; wheat, Thomson *et al.* 1992) plants, so that O₂ diffusion from the aerenchyma to the apex may be enhanced in roots with cuboidal packing of cortical cells.

Aerenchyma formation increases porosity above levels due to the usual intercellular spaces. Some dryland species, however, do not form aerenchyma (e.g. *Brassica napus*, Voesenek *et al.* 1999). In many wetland plants, aerenchyma is well developed even in drained conditions, and can be further enhanced in waterlogged conditions (Smirnov & Crawford 1983; Justin & Armstrong 1987). Aerenchyma is also extensive in submersed aquatic plants (Sculthorpe 1967; Schuette, Klug & Klomparens 1994) and seagrasses (Penhale & Wetzel 1983; Roberts, McComb & Kuo 1984). In submersed plants, O₂ evolved during photosynthesis in leaves, moves to the roots (Sorrell & Dromgoole 1987; Connell, Colmer & Walker 1999).

Porosity values for whole root systems or pooled adventitious roots for some species are given in Table 1. The constitutive aerenchyma in roots in aerobic environments and increases due to root zone O₂-deficiency, differ substantially among plant species (Table 1), even within a genus (e.g. 5–30% in *Rumex* species, Laan *et al.* 1989; 21–40% in *Carex* species, Visser *et al.* 2000a). Aerenchyma formation can also differ between genotypes within a species; for example, 19 versus 30% of cortical area in adventitious roots of two wheat cultivars (Huang, Johnson & Nesmith 1994). Furthermore, porosity can differ markedly between root types (e.g. wheat: 3% in seminal roots versus 22% in

Table 1. Porosity (% gas volume/tissue volume) in roots of selected non-wetland and wetland plant species grown in a drained/aerated or O₂-deficient root medium. Porosity includes the intercellular gas spaces and aerenchyma

Species		Porosity (%)		Reference no.
		Control	O ₂ -deficient	
Selected monocotyledonous non-wetland species				
<i>Triticum aestivum</i>	adventitious roots	3–6	13–22	1, 2, 3
<i>Hordeum vulgare</i>	adventitious roots	7	16	1
<i>Zea mays</i>	adventitious roots	4	13	4
<i>Festuca rubra</i>	entire root system	1	2	5
Selected dicotyledonous non-wetland species				
<i>Vicia faba</i>	entire root system	2	4	5
<i>Pisum sativum</i>	entire root system	1	4	5
<i>Brasica napus</i>	entire root system	3	3	6
<i>Trifolium tomentosum</i>	entire root system	7	11	7
Selected monocotyledonous wetland species				
<i>Oryza sativa</i>	adventitious roots	15–30	32–45	5, 8, 9, 10
<i>Typha domingensis</i>	adventitious roots	10–13	28–34	11, 12
<i>Phragmites australis</i>	adventitious roots	43	52	5
<i>Juncus effusus</i>	adventitious roots	31–40	36–45	5, 13
<i>Carex acuta</i>	adventitious roots	10	22	13
Selected dicotyledonous wetland species				
<i>Rumex palustris</i>	adventitious roots	15–30	32–45	5, 13
<i>Plantago maritima</i>	entire root system	8	22	5
<i>Ranunculus flammula</i>	entire root system	9–11	30–37	5, 14
Selected aquatic species (collected from natural habitats)				
<i>Zostera marina</i>	adventitious roots & rhizome		22–32	15
<i>Halophila ovalis</i>	adventitious roots		15	16

Growth conditions and references: 1, aerated or stagnant deoxygenated solution (McDonald *et al.* 2001a); 2, aerated or N₂-flushed solution (Thomson *et al.* 1990); 3, aerated or hypoxic solution (Thomson *et al.* 1992); 4, solutions continuously flushed with 40% O₂ in N₂ or with 5% O₂ and then not flushed (Drew *et al.* 1985); 5, drained or waterlogged compost (Justin & Armstrong 1987); 6, aerated or stagnant deoxygenated solution (Voesenek *et al.* 1999); 7, aerated or hypoxic solution (Gibberd *et al.* 1999); 8, drained or waterlogged soil (Armstrong 1971); 9, aerated or stagnant deoxygenated solution (Colmer *et al.* 1998); 10, redox-buffered solutions at +200 or –300 mV (Kludze, DeLaune & Patrick 1993); 11, redox-buffered solutions at +500 or –200 mV (Kludze & DeLaune 1996); 12, drained or waterlogged potting mix (Chabbi *et al.* 2000); 13, aerated or stagnant deoxygenated solution (Visser *et al.* 2000b); 14, drained or waterlogged sand (Smirnov & Crawford 1983); 15, sampled from a lagoon on the Alaskan Peninsula (Penhale & Wetzel 1983); 16, sampled from the Swan Estuary, Western Australia (Connell *et al.* 1999).

adventitious roots; McDonald *et al.* 2001a) and along roots (e.g. rice: 9% in root tips versus 45% in mature zones; Armstrong 1971).

Aerenchyma forms either by: (i) separation of cells ('schizogenous' aerenchyma); or (ii) collapse of cells ('lysigenous' aerenchyma) (Jackson & Armstrong 1999). The type of aerenchyma formed depends on plant species (Justin & Armstrong 1987) and tissue (Schussler & Longstreth 1996). The role of ethylene as the signal for the spatially selective programmed cell death in the cortex of roots of *Zea mays* during formation of lysigenous aerenchyma has been studied extensively (reviewed by Jackson & Armstrong 1999; Drew, He & Morgan 2000). However, the processes involved in formation of 'lysigenous' aerenchyma in roots of at least three wetland species (Longstreth & Borkhsenius 2000), may differ from those in *Zea mays*. Aerenchyma showing 'lysigenous-like features' contained cortical cells that elongated in the plane parallel to the root radius and shrunk in the perpendicular plane, to form large gas spaces (Longstreth & Borkhsenius 2000). In contrast to the detailed studies of lysigenous aerenchyma in roots of some species, very little is known about the processes

involved in formation of aerenchyma in other tissues, or about schizogenous aerenchyma formation, even in roots.

VENTILATION IN PLANTS: ROLES OF DIFFUSION AND THROUGH-FLOWS OF GASES

Diffusion is the mechanism by which O₂ moves within the plant body in most plant species (Armstrong 1979). However, through-flow of gases can occur in the lacunae of some floating-leaved and several emergent wetland species. Through-flow of gases raises O₂ concentrations in rhizomes above those supported via diffusion alone; often, levels are close to ambient (Armstrong *et al.* 1991, Armstrong J *et al.* 1992; Sorrell, Brix & Orr 1997; Vretare & Weisner 2000).

Through-flow of gases requires a pressure gradient between two ends of a pathway of low resistance, ending in an exit to the atmosphere (Beckett *et al.* 1988). Rates of flow are determined by the magnitude of the pressure gradient and the resistance to flow in the aeration system (Armstrong J *et al.* 1992; Brix *et al.* 1992). Pressures above

atmospheric levels in living shoot tissues (Dacey 1981; Schroder, Grosse & Woermann 1986; Mevi-Schutz & Grosse 1988b; Armstrong, Armstrong J & Beckett 1996a; b; Große 1996b; Steinberg 1996) and/or reductions below atmospheric at the end of dead culms (Armstrong J *et al.* 1992, 1996c), generate the pressure gradient (Fig. 1), depending on the species and environmental conditions. The volume of aerenchyma, organ cross-sectional area, and internal anatomy (e.g. presence of diaphragms) are some of the factors that determine resistance. In many wetland species, diaphragms interrupt the lacunae at stem nodes (Armstrong J & Armstrong 1988; Brix *et al.* 1992; Sorrell *et al.* 1997) and at root-rhizome junctions (Armstrong J & Armstrong 1988). The diaphragms contain pores and therefore generally have little effect on gas diffusion, whereas they do offer resistance to through-flows (Sorrell & Dromgoole 1987; Armstrong J & Armstrong 1988; Schuette *et al.* 1994;

Sorrell *et al.* 1997). Diaphragms guard against flooding of the aeration system; water ingress is restricted to a localized area if the rhizome is damaged (Armstrong J & Armstrong 1988; Soukup, Votrubova & Cizkova 2000).

Through-flows of gases in plants have been studied most extensively in the floating-leaved water lily, *Nuphar luteum* (Dacey 1980, 1981; Dacey & Klug 1982a, b), and the emergent wetland plant, *Phragmites australis* (Armstrong J & Armstrong 1990, 1991; Armstrong J *et al.* 1992, 1996c; Armstrong *et al.* 1996a, b; Beckett, Armstrong & Armstrong J 2001a). The potential for through-flow due to positive pressures generated in living tissues has also been demonstrated for other floating-leaved (Grosse, Buchel & Tiebel 1991) and emergent (Brix *et al.* 1992) wetland plants, whereas flows resulting from decreases in pressure (i.e. suction due to the venturi-effect at the end of dead culms) have so far only been documented in *Phragmites australis* (Armstrong

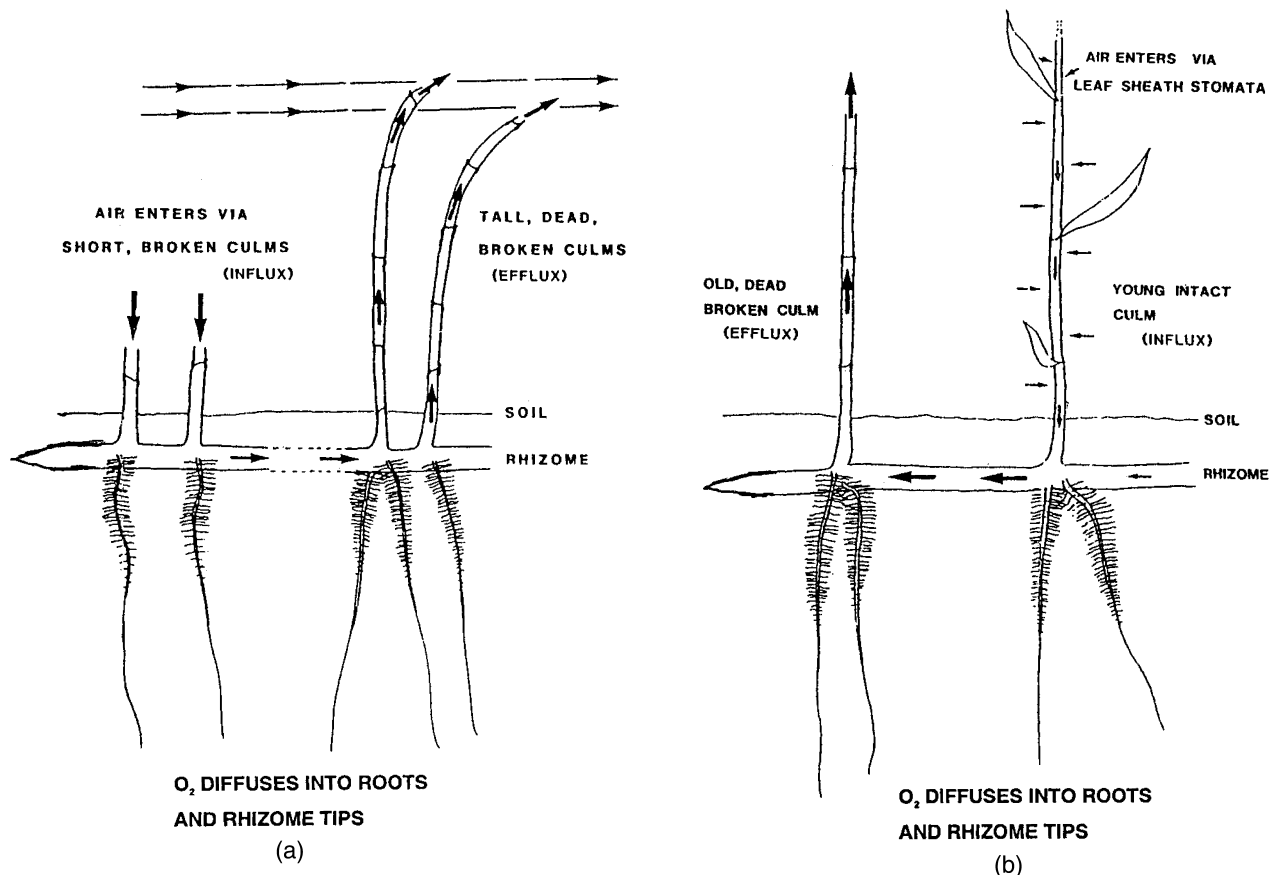


Figure 1. Sketches showing the through-flow pathways in *Phragmites australis*. (a) Flow depending on reductions in pressure causing 'suction'. Wind blowing across old, dead culms causes reduced pressure due to the 'venturi-effect'. (b) Flow depending on increases in pressure. Pressurization due to gradients in water vapour concentration across a microporous partition in leaf sheaths drives through-flow of gases. Large arrows indicate pressurized flows. (a) To date, only documented for *Phragmites australis*. (b) Documented for several emergent and floating-leaved species. In *Phragmites australis*, each mechanism can dominate under different environmental conditions, as influenced by season and time of day (see text). Examples of static pressure gradients and rates of through-flow are given in Table 2. Through-flow raises the O_2 concentration in rhizomes above that supported via diffusion alone, resulting in concentrations close to ambient levels. Movement of O_2 into and along roots, or during the final stages to rhizome tips (i.e. branches off the through flow-path) occurs via diffusion. Reproduced from Armstrong J *et al.* 1996c) with permission of the authors and Elsevier Science.

Table 2. Examples of pressurizations relative to atmospheric, and rates of gas flows in culms of *Phragmites australis* (emergent wetland species) and in the mid-rib and petiole of young leaves of *Nuphar luteum* (floating-leaved species). Data given are for selected field measurements

Conditions	Pressure differential ^a (Pa)	Flow rate ^b (mL min ⁻¹)
Venturi-induced through-flow in <i>Phragmites australis</i>		
¹ Winter in UK, 1–2 m culms, basal diameters 4–6 mm:		
Wind speed = 3 m s ⁻¹	– 2 to – 3 (static)	not determined
Wind speed = 5–6 m s ⁻¹	not determined	0.8
Through-flow due to pressurizations in living tissues in <i>Phragmites australis</i>		
² Sunny summer afternoon in UK, leafy culms ~2 m in height:		
(mid-afternoon, RH ~ 45%)	780 (static)	9.6
(sunset, RH ~ 92%)	100 (static)	0.3
³ Summer in Denmark	25–650 (static)	0.4–3.6
Through-flow due to pressurizations in living tissues in <i>Nuphar luteum</i>		
⁴ Mid-afternoon, Michigan, USA	175–260 (dynamic)	40–56

^a Static pressures were measured on excised organs with the usual ‘outlet’ blocked (e.g. connected to a pressure-measuring device), whereas dynamic pressures were measured in the organs while connected to the through-flow path.

^b A flow rate of 1 mL min⁻¹ equals a velocity of about 50 mm min⁻¹ along the culm of *Phragmites australis* (Armstrong J *et al.* 1992). Flows of 100 mm min⁻¹ can, depending on O₂ consumption rates in respiration, result in a ~100-fold increase in length of effective aeration along a channel (Armstrong *et al.* 1991).

References: ¹Armstrong J *et al.* (1992); ²Armstrong J & Armstrong (1991); ³Brix *et al.* (1996); ⁴Dacey (1981).

J *et al.* 1992, 1996c). The mechanisms involved in generating the pressure gradients are discussed in Appendix 1.

The magnitudes of the pressure gradients and through-flows in *Nuphar luteum* and *Phragmites australis* in selected field studies are given in Table 2. Static pressures are those measured in a system with flow blocked, whereas dynamic pressures are those measured without flow being restricted. The reasonably high flows, despite the relatively small pressure gradients generated via the venturi mechanism, when compared to the flows resulting from the much higher pressures in living tissues (Table 2), indicates that the resistance in the pathway for venturi-induced flows must be substantially lower than the resistance(s) in some part(s) of the pathway for flows resulting from positive pressures in living tissues.

Flow of gases via non-through-flow mechanisms have also been proposed; for example, in *Oryza sativa* (Raskin & Kende 1983; 1985). Such flows would, however, be small under steady-state conditions, so that the supply of O₂ to submerged tissues would increase only slightly (at most 1.06 times) above that via diffusion alone (Beckett *et al.* 1988; Armstrong *et al.* 1991). A second example is submerged plants, in which O₂ produced during photosynthesis may result in increased gas pressure in the lacunae, however, the lack of a through-flow pathway means O₂ movement in the steady-state condition will be via diffusion (Sorrell & Dromgoole 1988; Schuette *et al.* 1994). The exception being if inflorescences are present, then through-flow can occur in some species, because: (i) ebullition occurs when these become leaky after anthers dehiscence (Heilman & Carlton 2001); or (ii) spikes emerge making contact with the atmosphere (Schuette & Klug 1995), in each case providing exit pathways. When no exit pathway exists, the increased partial pressures of O₂ still enhance the

diffusion of O₂ from the shoots to the roots (Sorrell & Dromgoole 1987; Connell *et al.* 1999). For example in submerged rice seedlings, O₂ concentration at the root surface just behind the apex was 0.025–0.075 mol m⁻³ when light was provided to the shoots, but declined to 0.001 mol m⁻³ during the dark; resulting in diurnal variation in rates of root extension (Waters *et al.* 1989).

Even in those wetland plants with through-flow of gases in rhizomes, diffusion remains the mechanism for the movement of O₂ into and along roots (Beckett *et al.* 1988). The final pathway of O₂ movement to rhizome tips would also be diffusive (Armstrong J *et al.* 1992, 1996c; White & Ganf 1998). Through-flows, however, increase the O₂ concentration at the root-rhizome junction above that if only diffusion occurred in the shoot tissues, and thus enhances the diffusion of O₂ into the roots (Beckett *et al.* 1988; Armstrong J & Armstrong 1990; Armstrong J *et al.* 1992; Große & Bauch 1991). For example, in *Phragmites australis* through-flow increased O₂ concentration in the rhizome from ~ 9 to ~ 20%, resulting in an approximately four-fold increase in ROL from just behind the apex of an intact 113 mm adventitious root (Armstrong J *et al.* 1992).

O₂ diffusion in roots

Diffusion is the mechanism by which gases move into, and along, plant roots (Armstrong 1979; Beckett *et al.* 1988). The capacity for longitudinal O₂ diffusion in roots is determined by anatomical, morphological, and physiological characteristics, as well as environmental conditions such as temperature and demand for O₂ in the rhizosphere. Internal O₂ diffusion determines the maximum penetration of roots into anaerobic substrates (Armstrong 1979) and,

along with other factors (see below), influences rates of ROL to the rhizosphere.

Longitudinal O₂ diffusion in roots is enhanced by

- 1 The anatomical features of large aerenchymal lacunae, cuboidal packing of cortical cells, a proportionally large cortex, and a barrier to ROL exterior to the cortical aerenchyma (Yamasaki 1952; Armstrong 1979; Kawase 1981; Armstrong & Beckett 1987; Justin & Armstrong 1987). The first three factors enhance overall root porosity, whereas a barrier to ROL diminishes O₂ losses from the aerenchyma to the rhizosphere.
- 2 Morphological features such as thicker roots (Armstrong 1979; Armstrong, Healy & Webb 1982; Aguilar, Turner & Sivasithamparam 1999), small numbers of laterals (Armstrong, Healy & Lythe 1983; Sorrell *et al.* 2000), or if present short laterals that emerge close to the well aerated root base (Armstrong, Armstrong J & Beckett 1990) rather than further down the root.
- 3 Physiological traits, such as a lower demand for O₂ consumption in respiration (Armstrong 1979). Although rates of root respiration differ among species (Lambers, Scheurwater & Atkin 1996), there is no evidence to suggest waterlogging-tolerant plants have lower metabolic requirements for O₂ than intolerant ones (tissue mass basis). However, roots with large amounts of aerenchyma have lower respiration rates on a volume basis.
- 4 Environmental conditions, such as temperature. Cooler conditions decrease O₂ consumption along the diffusion path, by slowing respiration in root tissues (Armstrong 1979) and that by micro-organisms in the rhizosphere. Diffusivity of O₂ in the gas spaces being slowed much less than respiration rates as temperature declines; Q₁₀ of 1.1 for diffusivity versus 2–3 for respiration.

The roots of many (but not all) wetland species possess the anatomical features listed above. Depending on the species, some features are expressed constitutively and/or can be enhanced when plants are exposed to low O₂ in the root-zone. For examples, increased: (i) aerenchyma formation (Table 1); (ii) root thickness (Moog & Janiesch 1990; Visser *et al.* 2000a, b); and (iii) induction of a barrier to ROL (Section entitled 'Constitutive and inducible barriers to ROL' below). Moreover, root morphology (e.g. numbers of adventitious roots) may also be affected by root-zone O₂ deficiency, with responses differing among species (e.g. *Rumex* species, Laan *et al.* 1989; Visser *et al.* 1996).

Mathematical modelling indicated that several of the anatomical and morphological features listed above act synergistically to enhance O₂ diffusion to the apex of roots in anaerobic substrates (Armstrong 1979; Armstrong & Beckett 1987; Armstrong *et al.* 1990). Modelling has also indicated the importance of having a narrow stele to reduce the likelihood of O₂ deficiency, due to diffusion limitations, in this tissue of low porosity and with relatively high rates of O₂ consumption (Armstrong & Beckett 1987; Armstrong *et al.* 1994; Sorrell 1994). Adequate O₂ supply to the stele may be paramount because if O₂ deficiency does occur, solute transport to the shoot becomes impaired (Gibbs *et al.*

1998), and phloem transport of photosynthate to the roots would presumably also be reduced. Roots of many wetland species tend to have a narrow stele (Armstrong & Beckett 1987); for example, in adventitious roots of *Oryza sativa* the stele occupies less than 5% of the root cross-sectional area, whereas in *Sorghum bicolor* it occupies 24–36% (McDonald *et al.* 2002).

RADIAL O₂ LOSS FROM ROOTS

O₂ molecules within root aerenchyma will either be consumed by cells in adjacent tissues, diffuse towards the root apex, or diffuse radially to the rhizosphere and be consumed in the soil (Armstrong 1979). The flux of O₂ from the aerenchyma to the soil [termed radial O₂ loss (ROL)] is determined by the concentration gradient, the physical resistance to O₂ diffusion in the radial direction, and consumption of O₂ by cells along this radial diffusion path (Armstrong 1979; Armstrong & Beckett 1987). ROL can reduce markedly the supply of O₂ to the root apex (Armstrong 1979; Armstrong & Beckett 1987), with estimates up to 30–40% of the O₂ supplied via the root aerenchyma being lost to the soil (Armstrong 1979). When ROL occurs, it aerates the rhizosphere of plants growing in waterlogged soil (Armstrong 1979), resulting also in other significant changes in the soil chemistry within the rhizosphere. For example, nutrient availability (Reddy, Patrick & Lindau 1989; Saleque & Kirk 1995; Kirk & Bajita 1995; Christensen & Wigand 1998); concentrations of potentially toxic reduced soil substances (Laanbroek 1990; Begg *et al.* 1994; Mendelssohn, Keiss & Wakeley 1995; St-Cyr & Campbell 1996), and microbial populations (Gilbert & Frenzel 1998), are all profoundly influenced by ROL from roots.

Methods used to evaluate ROL from roots

Several methods have been used to evaluate ROL from roots (Table 3). Analyses of oxidized minerals coating roots (mainly Fe plaques) (e.g. Mendelssohn & Postek 1982) and *in situ* measurements of increased redox in sediments containing plant roots (e.g. Carpenter, Esler & Olsen 1983) provide valuable evidence for ROL in field situations. Mechanistic interpretations based on field measurements are, however, complicated by the complexity of environmental (above- and below-ground conditions) and biological (plant and soil microbial) factors interacting to produce a 'net' result. Laboratory studies have made use of several techniques (see below) to evaluate the effects of environmental parameters (e.g. depth of partial submergence, temperature, light, root-zone redox potential) and plant physiological processes (e.g. acclimation to root-zone hypoxia, root porosity, genotype) on ROL from roots.

Studies using indicator dyes, such as reduced/oxidized methylene blue, in stagnant deoxygenated agar solutions (e.g. Armstrong J & Armstrong 1988) or in pots of waterlogged soil (Armstrong J *et al.* 1992) provide qualitative information on spatial patterns of ROL. Redox potential

Table 3. Summary of methods used to assess various aspects of radial O₂ loss (ROL) from plant roots (for explanations see text)

Method	Advantages	Disadvantages	Example of use
Iron plaques on roots			
– soil	Roots sampled from field grown plants, spatial assessments at cell/tissue level using X-ray microanalysis	Destructive and indirect measure, expensive, time-consuming, static view at one point in time	Mendelsohn & Postek (1982)
– solution	Spatial resolution, composition of root bathing medium controlled	As above	Green & Etherington (1977)
Root-plane	Study of root/soil interface, control of some soil conditions	Root characteristics may differ from those in undisturbed, soil-grown plants	Begg <i>et al.</i> (1994)
Sediment redox potential	Field measurements <i>in situ</i> , monitor temporal (diel and seasonal) patterns	Difficult to control/modify the influence of environmental conditions	Carpenter <i>et al.</i> (1983)
Reduced/oxidized dyes (e.g. methylene blue)	Spatial resolution, quick, inexpensive	Qualitative, low sensitivity, possible toxicity of reducing agents	Armstrong J & Armstrong (1988)
Net uptake or loss of O ₂ to bathing medium (closed or flow-through)	Whole plant measurements	Lack of irreversible O ₂ sink provides opportunity for re-absorption of O ₂ by roots and therefore underestimates ROL	Sorrell & Armstrong (1994)
Titrimetric methods e.g. Ti ³⁺ -citrate(closed, flow-through, or automatic titration)	Whole plant measurements, mimics –ve redox potential in soils and this aspect of soil O ₂ demand, estimates O ₂ flux	Lack of spatial resolution, difficulties in meaningful expression of results (e.g. per plant, per root wt or surface area) for treatment or species comparisons, possible adverse effects of citrate	Kludze <i>et al.</i> (1994) Sorrell (1999)
Root-sleeving O ₂ electrodes	High spatial and temporal resolution, mimics soil O ₂ consumption (only at the position of measurement), direct measure of O ₂ fluxes from individual intact roots, short (min) and longer (d) term responses can be monitored, other parameters of interest can be calculated from primary data	Measurements only of individual roots, strong O ₂ sink (i.e. O ₂ consumption) only at the position within the electrode	Armstrong (1964) Armstrong (1979) Armstrong & Wright (1975)
O ₂ microelectrodes			
– soil	Measurements of conditions in the ‘natural’ substrate, monitor diel patterns, high temporal and spatial resolution	Disturbance during collection of ‘sediment blocks’, exact location of the sensor relative to the roots not known, equipment expensive and somewhat fragile	Pedersen <i>et al.</i> (1995)
– solution	Excellent spatial and temporal resolution, tissue and external measurements enable O ₂ concentration gradients to be assessed	Construction requires skill and is time-consuming, no strong O ₂ sink, electrodes fragile	Armstrong <i>et al.</i> (2000)
Mathematical models	Provides theoretical basis, gaps in knowledge identified	Limited by assumptions and data available to test the models	Luxmoore <i>et al.</i> (1970) Armstrong (1979) Armstrong & Beckett (1987)

measurements in pots of soil with, or without, plants have provided a quantitative comparison of the capacity for ROL among species (Justin & Armstrong 1987). Measurements of O₂ net fluxes from whole root systems bathed in

low O₂ solutions (e.g. Bedford, Boudin & Beliveau 1991) may give erroneous results as O₂ lost from some regions may be re-absorbed by other parts of the root system, resulting in an underestimation of ROL (Sorrell & Arm-

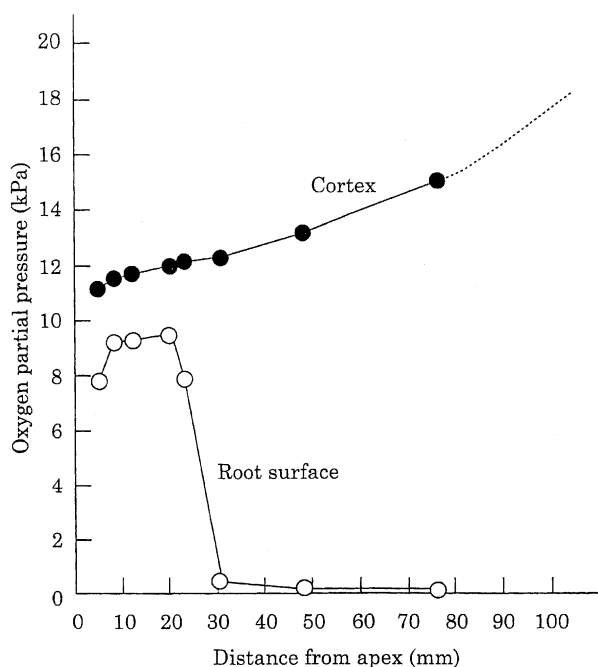


Figure 2. O_2 partial pressures within the cortex and at the root surface of an intact 100 mm root of *Phragmites australis*, measured using an O_2 microelectrode. Shoots were in air and the roots were in an O_2 -free solution containing 0.05% agar to prevent convection in the solution. The cortical O_2 concentration increases towards the root-rhizome junction, a pattern consistent with O_2 diffusion down the root. In contrast, O_2 at the root surface is highest near the root tip and declines markedly at positions more basal than 30 mm, indicating a decline in radial O_2 loss (ROL) in these more basal zones. The decline in ROL in basal root zones occurs despite the higher internal O_2 concentrations providing a larger gradient for O_2 loss, indicating substantial increases in the resistance (i.e. decreased permeability) to O_2 diffusion through cell layer(s) between the aerenchyma and the root exterior. Reproduced from Armstrong *et al.* (2000) with permission of the authors and Academic Press.

strong 1994). Titrimetric methods making use of reducing agents (e.g. Ti^{3+} -citrate) added to solutions bathing intact root systems, may mimic soil O_2 demands and also scavenge O_2 lost to the solution preventing its re-absorption, thereby providing better estimates of ROL (Sorrell & Armstrong 1994; Kludze, DeLaune & Patrick 1994). However, the proportion of O_2 lost from different regions of the root system can differ markedly (Figs 2 & 3); ROL in many wetland species is highest from the root tips and numerous short laterals (e.g. Armstrong 1964; Conlin & Crowder 1989; Armstrong *et al.* 1990; Sorrell 1994; Armstrong *et al.* 1996c). Therefore, the majority of O_2 loss may occur from only a small proportion of the root system, so results expressed on the basis of whole root systems provide a poor approximation of the actual situation at the sites of ROL.

The root-sleeving O_2 electrodes developed by Armstrong (1964, 1967, 1994) enable ROL measurements of high spatial (several millimetres) and temporal resolution along individual roots; thus overcoming the problems listed

above. Measurements along selected roots of intact plants are taken with shoots in air and roots in stagnant deoxygenated solution containing 0.05–0.1% agar, to prevent convection in the solution, so that the O_2 sink of the medium is essentially removed everywhere except at the electrode. This situation is still not ideal, because rates of ROL measured in the absence of competing external sinks along the root are likely to be higher than without such competition for O_2 . Experiments using multiple root-sleeving O_2 electrodes simultaneously positioned along the same root would, at least to some degree, address this issue.

Measurements using O_2 microelectrodes have provided even higher spatial resolution (several micrometres) than the root-sleeving O_2 electrodes (Armstrong *et al.* 2000). However, unlike the root-sleeving electrodes that measure O_2 flux, the microelectrodes measure O_2 concentration. Fluxes can be calculated from profiles of O_2 concentrations measured in the unstirred boundary layer adjacent to roots, but would underestimate ROL if measured in the absence of a well-defined sink for O_2 at a known distance from the root surface (Armstrong *et al.* 2000). The O_2 microelectrodes, inserted into blocks of sediments containing intact plants, have also been used to study diel changes and spatial patterns of O_2 loss from roots of submersed plants (Pedersen, Sand-Jensen & Revsbech 1995).

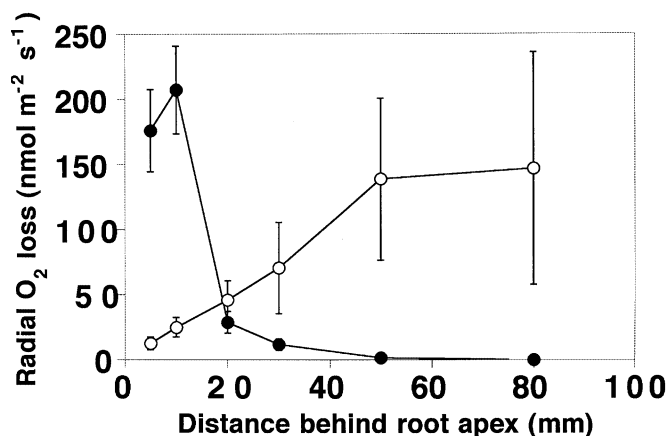


Figure 3. Rates of radial O_2 loss (ROL) along intact adventitious roots of *Oryza sativa* L. (cv. Calrose) when in an O_2 -free root medium with shoots in air, at 30 °C. Plants were raised in either aerated (open symbols) or stagnant deoxygenated nutrient solution (closed symbols) before the measurements were taken along 118–130 mm adventitious roots ($n = 3 \pm$ standard errors) of 28- to 29-day-old plants. The O_2 -free root medium used during ROL measurements contained 5.0 mol m⁻³ KCl, 0.5 mol m⁻³ CaSO₄, and 0.1% (w/v) agar to prevent convection. Seedlings were raised in aerated solution for 14 d, after which treatments were imposed for the final 14–15 d, for plants in a 30/25 °C (day/night) growth chamber. The composition of the nutrient solution was as described in McDonald *et al.* (2001a). Porosity in bulk samples of adventitious roots was ($n = 3 \pm$ standard errors): aerated, 21.9 ± 1.4; stagnant, 36.5 ± 1.0. Extension rates for intact adventitious roots grown as described above, and of lengths similar to those used in the measurements were: aerated, 34.3 ± 1.9 mm d⁻¹; stagnant 28.5 ± 2.0 mm d⁻¹. Data from own experiments.

Mathematical modelling (Luxmoore, Stolze & Letey 1970; Armstrong 1979; Armstrong & Beckett 1987) has improved the mechanistic understanding of internal aeration processes and ROL from individual roots in anaerobic substrates. The development of models to 'scale up' ROL measurements taken for individual roots, to represent whole root systems, should be considered.

Adaptive significance of a barrier to ROL for roots in anaerobic substrates

Adventitious roots of many wetland species contain a barrier to ROL in the basal zones (Armstrong 1964, 1971; Smits *et al.* 1990; Koncalova 1990; Jackson & Armstrong 1999; Armstrong *et al.* 2000; Visser *et al.* 2000b; McDonald *et al.* 2002) and a barrier to ROL has also been shown in roots of a sea grass (Connell *et al.* 1999). A barrier to ROL in basal root zones can enhance longitudinal O₂ diffusion in the aerenchyma towards the apex, by diminishing losses to the rhizosphere.

Figure 2 shows the marked effect of a barrier to ROL on O₂ concentrations along the surface of a *Phragmites australis* adventitious root when in a deoxygenated root medium. Root surface O₂ concentrations were relatively high near the tip, whereas in regions more basal than 30 mm behind the apex, O₂ at the root surface was extremely low. The low O₂ at the root exterior in basal zones occurred despite the progressively higher O₂ concentrations within the cortex of the root for locations closer to the root/shoot junction (Fig. 2). Thus, even though the concentration gradient for ROL had increased, the resistance in outer cell layers was so high (i.e. permeability was very low) so as to prevent ROL. The curvilinear gradient in O₂ concentration down the root is

consistent with planar diffusion down a tube in which O₂ is removed (e.g. consumed in respiration) along the length of the diffusion path; a process modelled by Armstrong (1979).

Not all wetland species, however, have a 'tight' barrier to ROL (Smits *et al.* 1990; Chabbi, McKee & Mendelssohn 2000; Visser *et al.* 2000b). Examples of differences in the degree to which the outer cell layers of roots remain permeable to O₂ are given in Table 4. A major deficiency in knowledge is a lack of data on permeability coefficients for O₂ diffusion across the cell layers exterior to the aerenchyma. This limits understanding of the mechanisms controlling ROL and prevents a truly quantitative comparison of the radial permeability to O₂ in the outer cell layers of roots of different species, or under various treatments. Nevertheless, it is clear that rates of ROL from basal root zones differ markedly among wetland species. Possible explanations for such species differences are: (i) the importance of a barrier to ROL for effective longitudinal diffusion of O₂ in roots diminishes as the volume of aerenchyma, and/or root diameters, become large (Armstrong 1979); (ii) wetland species that inhabit substrates that do not become highly reduced (e.g. low in organic matter, Smits *et al.* 1990; flowing water, Armstrong & Boatman 1967) may have roots with less resistance to ROL than those from more reducing substrates; (iii) shallow rooting may be all that is necessary for plants in some habitats (e.g. nutrient-rich, permanent wetlands); and (iv) differences in developmental stage or types of roots measured. Regarding developmental stage; ROL was evident from the main axis of short, young roots of *Typha latifolia* and *Phragmites australis*, whereas in older, longer roots ROL from the basal zones of the main axis was restricted (Conlin & Crowder 1989).

Species	Habitat	ROL (nmol m ⁻² s ⁻¹)		'Type' of barrier to ROL
		Distance behind apex		
		5 mm	60–80 mm	
¹ <i>Oryza sativa</i>	W	175	< 1	'tight'
² <i>Phragmites australis</i>	W	390	10	'tight'
³ <i>Hordeum marinum</i>	W	273	24	'tight'
⁴ <i>Rumex palustris</i>	W	45	50	'partial'
⁵ <i>Phalaris aquatica</i>	W	300	300	'partial'
⁶ <i>Triticum aestivum</i>	NW	81	179	'weak'
⁷ <i>Hordeum vulgare</i>	NW	104	218	'weak'

Habitats: W, wetland; NW, non-wetland.

Permeability coefficients are not available for O₂ diffusion across the cell layers exterior to the aerenchyma. Therefore, the descriptions of 'tight', 'partial' or 'weak' have been used to describe the barrier to ROL in various species. As internal O₂ concentrations increase towards the root-shoot junction (Fig. 2): (i) a 'tight' barrier is indicated by very low ROL from mature zones, but high rates near the root tip; (ii) a 'partial' barrier results in similar rates of ROL along a root; and (iii) a 'weak' barrier results in ROL being much higher in more basal zones, than near the root tip.

Sources: ¹roots 118–130 mm, grown in deoxygenated stagnant solution (Data from Fig. 3);

²roots 90–170 mm, grown in waterlogged compost (Armstrong J & Armstrong 2001b);

^{3,6,7}roots 100–120 mm, grown in deoxygenated stagnant solution (McDonald *et al.* 2001a);

⁴roots 100–160 mm, grown in deoxygenated stagnant solution (Visser *et al.* 2000b); ⁵roots 100–140 mm, grown in deoxygenated stagnant solution (McDonald *et al.* 2002).

Table 4. Rates of radial O₂ loss (ROL) measured just behind the tip and from more basal zones of intact adventitious roots of selected species grown in a O₂-deficient rooting medium.

Regarding root types; root dimorphism (e.g. 'aquatic' and 'soil' roots or 'superficial' and 'deeper' soil roots) is common in wetland plants, and these root types can differ in internal aeration characteristics (Sorrell 1994; Sorrell *et al.* 2000), and may also differ in ROL.

Several workers have suggested ROL is of adaptive significance for plants growing in waterlogged soil, because an oxidized rhizosphere may 'protect' roots against soil-derived toxins (e.g. Green & Etherington 1977; Armstrong 1979; Jaynes & Carpenter 1986; Koncalova 1990; Chabbi *et al.* 2000), even though ROL reduces the supply of O₂ to distal root tissues (Armstrong 1979). This role for O₂ leakage into the rhizosphere may, at first, appear contradictory to the notion that a barrier to ROL is an adaptive feature in roots of wetland plants. However, once the importance of spatial patterns of ROL within a whole root system are recognized, these views are easily reconciled. Roots of species with a 'tight' barrier to ROL in basal zones can have high rates of ROL near the root tip (Armstrong 1964, 1971; Armstrong *et al.* 1990; Visser *et al.* 2000b) and also from numerous short laterals which emerge near the base of the main axes (Conlin & Crowder 1989; Armstrong *et al.* 1990; Sorrell 1994). The dense laterals with overlapping rhizospheres and high rates of ROL may enable an oxidized zone to persist even when O₂ is consumed by soil microorganisms. This combination of anatomical (aerenchyma, 'tight' barrier to ROL in basal zones) and morphological (short, O₂ permeable laterals near the root base) features enhances root penetration into anaerobic sediments, and also allows an oxidized rhizosphere at key locations. ROL may protect the apex and laterals from reduced soil toxins, whereas a physical barrier near the root exterior in mature zones presumably restricts entry of soil toxins in these regions (suggested by Armstrong 1979; Armstrong J *et al.* 1996c).

Mathematical modelling of root growth as a function of internal O₂ diffusion, supports the view that a barrier to ROL is beneficial for the penetration of roots into anaerobic substrates (Armstrong 1979). Modelling has also been used to assess the influence of O₂ consumption and loss from laterals, on the penetration of the main root axis. If laterals emerge near the root base, the diffusion path length is relatively short so that ROL from these laterals would not have a marked affect on O₂ concentrations in the root base, so O₂ diffusion down the main axis is almost maintained; a scenario observed for *Phragmites australis* (Armstrong *et al.* 1990). In contrast, if laterals are distributed more evenly along the main axis, rather than as a cluster near the root base, O₂ supply to the primary root apex would be reduced significantly by the development of laterals (Sorrell *et al.* 2000); a situation documented experimentally for non-wetland species with roots of relatively low porosity (Armstrong *et al.* 1983; Gibberd, Colmer & Cooks 1999). Wetland species differ in the numbers of lateral roots formed along adventitious roots, being absent in some species but relatively dense in others (Sorrell *et al.* 2000; Bouma *et al.* 2001). The laterals formed along adven-

titious roots tend to be much shorter, thinner, and of lower porosity than the main axes (Sorrell *et al.* 2000; Bouma *et al.* 2001), and the laterals may be the major source of O₂ loss to the rhizosphere in some species (Armstrong *et al.* 1990). Data on the distributions of laterals along adventitious roots of wetland species are generally lacking, so knowledge on the consequences of laterals for aeration and penetration of the main axes of adventitious roots in wetland plants is restricted to the few species discussed above.

In contrast to the many wetland species that have a 'tight' barrier to ROL, none of the dryland crop species examined to date had this feature; for examples, *Triticum aestivum* (Thomson *et al.* 1992), *Brassica napus* (Voesenek *et al.* 1999), *Trifolium tomentosum* (Gibberd *et al.* 1999), *Hordeum vulgare* and *Secale cereale* (McDonald *et al.* 2001a), *Sorghum bicolor* and *Avena sativa* (McDonald *et al.* 2002). Recently, McDonald *et al.* (2001a) (see also Table 4) described a barrier to ROL in adventitious roots of the marsh species *Hordeum marinum* (syn. *Critesion marinum*) a 'wild' relative of waterlogging-sensitive crops in the Triticeae (i.e. *Triticum aestivum* and *Hordeum vulgare*). Root penetration into waterlogged soil was superior in *Hordeum marinum*, compared with *Triticum aestivum* (namely 210 versus 127 mm), even though root porosity in the two species was similar (namely 22–25%). Deeper roots should enhance soil exploration for nutrients during waterlogging, but may also offer an important competitive advantage for re-growth of a deep root system once the water level recedes in transiently waterlogged soils.

Anatomical and physiological basis of the barrier to ROL in roots

Information on the anatomical basis (and chemical composition) of barriers to ROL in plant roots is scant. In *Oryza sativa*, the barrier to ROL may result from a layer of sclerenchymatous fibres with thick secondary walls on the external side of the cortex, which becomes the exodermis as roots age (Clark & Harris 1981). In addition, cells in the outer tissues of roots of some species can be packed so closely that gas spaces are extremely small or even non-existent (Justin & Armstrong 1987; Armstrong *et al.* 1991), resulting in high impedance to O₂ diffusion in the radial direction. In *Phragmites australis* (Armstrong J & Armstrong 1988; Armstrong *et al.* 2000) and *Eleocharis sphacelata* (Sorrell 1994) a combination of densely packed cells in low porosity hexagonal arrangements, suberin deposits, and lignification in the outer cell layers, may form the barrier to ROL. Profiles of O₂ concentrations across adventitious roots of *Phragmites australis*, measured using microelectrodes, showed the greatest impedance to ROL occurs in the hypodermis (Armstrong *et al.* 2000). The O₂ consumption in the exterior cell layers may also reduce ROL from roots (Armstrong *et al.* 2000); nevertheless, a barrier to ROL was evident in adventitious roots of *Oryza sativa* even when respiration was inhibited by cooling the root medium

to 3 °C (Armstrong 1971), confirming a large physical impedance to radial O₂ diffusion.

In addition to the species discussed in the preceding paragraph, roots of other wetland species also contain a hypodermis with suberized walls and/or a thickened exodermis; these features may provide mechanical support for roots containing large amounts of aerenchyma (Seago *et al.* 1999, 2000), in addition to a possible role in restricting ROL. Furthermore, root-zone O₂ deficiency can enhance thickening of the cell walls in the exodermis in roots of some species, for example *Carex remota* (Moog & Janiesch 1990).

A physical barrier to ROL may be of adaptive significance for wetland plants, but may also have drawbacks for some root functions. Armstrong (1979) and Koncalova (1990) hypothesized this feature may impede water and nutrient uptake. The few available studies support the notion that exodermal/hypodermal layers with thickened cell walls (features that may form the barrier to ROL) restrict uptake of water and nutrients. Diffusive permeability of water, phosphate and calcium were 200- to 500-fold lower across exodermal/hypodermal layers isolated from *Carex arenaria*, when compared to the permeability of layers isolated from onion roots (Robards, Clarkson & Sanderson 1979). In roots of *Oryza sativa*, hydraulic conductivity in the radial direction was 0.2–0.5 of that in *Zea mays* when measured using a root pressure probe and hydrostatic pressure gradients (Miyamoto *et al.* 2001), and rates of NH₄⁺ and NO₃⁻ net uptake in the basal regions were about 30% of those in *Zea mays* (Colmer & Bloom 1998), even when the plants were grown in aerated solutions. Whether, or not, having a barrier to ROL affects the movement of substances other than O₂ (e.g. water, nutrients, soil toxins, soil-derived gases) between roots and soil would be determined by the anatomical and chemical nature of the barrier (Beckett, Armstrong & Armstrong J 2001b), as well as the possibility of ‘passage areas’ (Armstrong *et al.* 2000). Alternatively, lateral roots may be the main surface for nutrient and water uptake by wetland species (suggested by Sorrell & Orr 1993; Armstrong J *et al.* 1996c).

Constitutive and inducible barriers to ROL

Roots of some wetland plants have an inducible barrier to ROL; the basal zones remain permeable to ROL when grown in aerated conditions but growth in stagnant deoxygenated solution induced a ‘tight’ barrier to ROL. Figure 3 shows this phenomenon in adventitious roots of *Oryza sativa*. Induction of a ‘tight’ barrier to ROL by growth in stagnant solution occurred in adventitious roots of a diverse range of rice genotypes (Colmer *et al.* 1998; Colmer 2002), *Hordeum marinum* (McDonald *et al.* 2001a), and *Lolium multiflorum* (McDonald *et al.* 2002). A partial barrier to ROL was also induced in adventitious roots of *Caltha palustris* (Visser *et al.* 2000b). In contrast to the inducible barrier to ROL in adventitious roots of *Oryza sativa* and some other wetland species, a ‘tight’ barrier to ROL was

constitutively present in the adventitious roots of many other wetland species (e.g. *Juncus effusus*, *Echinochloa crus-galli*, *Eleocharis acuta*, and others) (Visser *et al.* 2000b; McDonald *et al.* 2002), but only a ‘partial’ barrier to ROL was evident in others (e.g. *Lophopyrum elongatum*, McDonald, Galwey & Colmer 2001b; *Rumex palustris*, Visser *et al.* 2000b).

The signal(s) involved in induction of the barrier to ROL remain to be elucidated. For roots of *Oryza sativa*, we (Colmer, Cox and Voesenek, unpublished) have evaluated the potential role of ethylene. In our experiments, exogenously applied ethylene (0.2 or 2.0 μL L⁻¹) enhanced aerenchyma formation (see also Justin & Armstrong 1991), but not the ‘tight’ barrier to ROL (data not shown). Recently, it was shown that carboxylic acids (e.g. acetic, propanoic, and butyric acids; phytotoxins produced by micro-organisms in waterlogged soils) applied to roots of *Oryza sativa* or *Phragmites australis* caused lignification and suberization in the walls of cells in the outer layers, resulting in a marked decline in ROL from regions (fine lateral roots and apical few centimetres) that are ‘normally permeable’ to ROL (Armstrong J & Armstrong 2001b). However, these responses to carboxylic acids may result from injury (see Armstrong J & Armstrong 2001a), rather than being a specific signal for induction of the barrier to ROL.

Given the possible drawbacks of having a ‘tight’ barrier to ROL on nutrient and water uptake (Section entitled ‘Anatomical and physiological basis of the barrier to ROL in roots’ above), it is tempting to speculate that an inducible barrier to ROL may be of adaptive significance to plants inhabiting transiently waterlogged soils and/or contribute to the physiological plasticity that may enable some species (e.g. *Oryza sativa*) to grow in diverse environments ranging from drained to flooded soils. Further work is required to determine if the type of barrier to ROL formed (‘tight’ or ‘weak’, constitutive or inducible) is associated with any niche wetland habitat (e.g. frequency or duration of waterlogging; severity of declines in soil redox potential).

MOVEMENT OF GASES OTHER THAN O₂ (ETHYLENE, CO₂, METHANE)

Development of aerenchyma not only enhances O₂ movement to submerged tissues, but also promotes venting of gases from these tissues to the atmosphere. Ethylene (Visser *et al.* 1996) and CO₂ produced in the roots or in the soil by micro-organisms (Smith & Russell 1969), as well as other gases (e.g. methane) produced in the soil (Smith & Restall 1971), are entrapped by the water layers and can build up to relatively high concentrations in the roots. These gases diffuse upwards in the aerenchyma to the shoots, or to the rhizome and then subsequently to the shoot via through-flow, depending on the species (Jackson & Campbell 1975; Dacey 1979; Dacey & Klug 1982a; Higuichi, Yoda & Tensho 1984; Sebacher, Harriss & Bartlett 1985; Sorrell & Boon 1994; Brix, Sorrell & Schierup 1996;

Shannon *et al.* 1996; Butterbach-Bahl, Papen & Rennenberg 1997; Yavitt & Knapp 1998).

Venting of ethylene is of interest because endogenous levels of this phytohormone have marked effects on root growth and development (Jackson 1991), including formation of lysigenous aerenchyma (Jackson & Armstrong 1999). Ethylene at low concentrations (0.02–0.1 $\mu\text{L L}^{-1}$) can enhance root extension in some species, but higher concentrations (> 0.1 $\mu\text{L L}^{-1}$) inhibit root growth (Smith & Robertson 1971; Konings & Jackson 1979; Visser *et al.* 1997). Thus, venting of ethylene from roots in waterlogged soil, via the aerenchyma, may reduce the likelihood of the gas accumulating to concentrations that inhibit root growth (Visser *et al.* 1997). Moreover, root-derived ethylene (and/or its precursor 1-aminocyclopropane-1-carboxylic acid (ACC) after being converted to ethylene in the shoots) also invokes physiological responses in the shoots of waterlogged plants; such as leaf epinasty (e.g. tomato, Jackson & Campbell 1975), lysigenous aerenchyma formation in shoot tissues (e.g. *Zea mays*, Jackson 1989), and adventitious rooting (e.g. several species, Jackson & Campbell 1975; Drew *et al.* 1979; Liu, Mukherjee & Reid 1990; Visser *et al.* 1996). Other root-borne signals may also influence shoot physiology of waterlogged plants (Jackson 1994).

CO_2 from sediments moves via the roots to the shoots and provides substrate for photosynthesis in some submersed aquatic plants (Raven, Osborne & Johnston 1985; Raven *et al.* 1988; Pedersen & Sand-Jensen 1992); and presumably may also, together with CO_2 produced in respiration, supplement the uptake of dissolved inorganic carbon from the water (Madsen & Sand-Jensen 1991) in other submersed plants. In emergent wetland species, the partial pressure of CO_2 in leaf gas spaces can be one order of magnitude higher than in the atmosphere (Constable, Grace & Longstreth 1992), and CO_2 from the aerenchyma can be fixed in photosynthesis (Constable & Longstreth 1994). This CO_2 may be derived from the sediments (Higuchi *et al.* 1984; Brix 1990) and/or from respiration in submerged rhizomes and root tissues. In floating-leaved plants, CO_2 produced in the sediments or root tissues moves to the shoots where up to 85% of the CO_2 in the lacunae may be fixed via photosynthesis, the remainder presumably being lost to the atmosphere (Dacey 1980; Dacey & Klug 1982a). Moreover, venting of CO_2 from the roots via the aerenchyma may reduce the risk of asphyxiation of root cells (Jackson & Armstrong 1999); although sensitivity to high root-zone CO_2 (2 to >10%) may differ among species (Stolwijk & Thimann 1957; Bouma *et al.* 1997 and references therein), and even between genotypes within a species (e.g. wheat cultivars, Huang *et al.* 1997). The quantitative significance of soil- and root-derived CO_2 for inhibition of root growth, as well as the contributions of each of these CO_2 sources as substrate for photosynthesis, should be determined for a wider range of plants when in waterlogged soils.

Emissions of methane from rice paddy fields and wetlands are major sources of this trace gas to the atmosphere (Matthews, Fung & Learner 1991; Bartlett & Harriss 1993). Interest in the processes involved in methane production

and release from wetlands has increased dramatically in recent years, due to the proposed role of methane as a 'greenhouse gas' (Lelieveld, Crutzen & Bruhl 1993). Consideration of the factors that affect rates of net methane production by micro-organisms in anaerobic soils is beyond the scope of this review, as is the impact of plant-mediated processes on methane production (see Frenzel, Rothfuss & Conrad 1992; Beckett *et al.* 2001b). Rather, the role of wetland plants as a route for methane escape from waterlogged soils, via the aerenchyma, to the atmosphere is highlighted here. Up to 90% of methane emissions from waterlogged soils may occur via the plant-mediated conduit between soil and atmosphere (Shannon *et al.* 1996). Plant-mediated emissions of methane have been documented for floating-leaved and emergent wetland plants with through-flows (Dacey 1979; Sebacher *et al.* 1985; Sorrell & Boon 1994; Brix *et al.* 1996; Chanton & Whiting 1996; Yavitt & Knapp 1998) and in emergent wetland plants with internal aeration via diffusion (Cicerone & Shetter 1981; Nouchi, Mariko & Aoki 1990; Butterbach-Bahl *et al.* 1997). Thus, long-distance gas transport not only affects the individual plant, but may also contribute to processes of ecological importance for planet Earth.

FUTURE DIRECTIONS

Much remains to be learnt regarding root structure and function in wetland plants (cf. Seago *et al.* 2000). The integration of modelling and physiological approaches has provided a sound quantitative framework for studies of root aeration, yet some critical experimental data are lacking; for example, permeability coefficients for O_2 diffusion across the exodermal/hypodermal layers for different species and for different positions behind the root apex. The mechanism(s) responsible for barriers to ROL also need to be more clearly elucidated; studies using a combination of techniques from microscopy and analytical chemistry (cf. Zeier *et al.* 1999) would be particularly useful. The signal(s) and subsequent cascade of events involved in the formation of inducible barriers to ROL also remain to be determined. Knowing how to manipulate expression of this trait will aid further experimentation on this phenomenon, and contribute to identification of its genetic regulation. In addition to root aeration processes, other aspects of root physiology in wetland plants also require further investigation. For examples, transport physiology of water and nutrients, and the regulation of influx of soil-derived toxins (e.g. reduced metal ions as well as microbial metabolites such as carboxylic acids) and gases (e.g. methane, CO_2 , and ethylene), should be priority areas for future work. These factors are of particular importance to understanding the ecophysiology of wetland species and wetland ecology.

Root aeration is determined by a combination of traits, but knowledge on the genetic basis of these is scant. Mutants, or transgenic plants, for the root aeration traits of interest (e.g. aerenchyma, barrier to ROL) are not available at this time. 'Wide-crossing' between dryland crop species

and selected 'wild' relatives from wetland habitats may provide a system for studies of the genetic basis and physiological consequences of key traits (e.g. *Hordeum marinum* is a marsh species with a barrier to ROL, whereas *Triticum aestivum* lacks this trait). If our current attempts (Islam and Colmer, unpublished) to hybridize *Hordeum marinum* with *Triticum aestivum* are successful, we aim to produce disomic addition lines with individual *Hordeum marinum* chromosomes in wheat. Such addition lines may enable studies on the genetic basis and physiological consequences of a barrier to ROL, as expressed in the background of waterlogging-sensitive *Triticum aestivum*. We are encouraged by the success achieved in previous attempts to hybridize *Hordeum* species with *Triticum aestivum* (Islam, Shepherd & Sparrow 1981; Islam & Shepherd 1990), including *Hordeum marinum* (Jiang & Dajun 1987; Islam and Colmer, unpublished). Similarly, *Zea mays* × *Zea luxurians* and *Zea mays* × *Tripsacum dactyloides* hybrids have provided a system for studies of constitutive root aerenchyma (Ray *et al.* 1999); but whether these 'wild' relatives of maize also contain a barrier to ROL was not evaluated. Moreover, subsequent cytogenetic manipulations of these hybrids (e.g. development of recombinant lines), may enable improvement of root aeration characteristics, and presumably waterlogging tolerance, in some dryland crops.

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APPENDIX 1: MECHANISMS GENERATING PRESSURE GRADIENTS, AND THROUGH-FLOW OF GASES, IN SOME WETLAND PLANTS

Flows arising from venturi-induced 'suction'

Through-flow of gases in the aerenchymatous rhizomes of *Phragmites australis* can be driven by reductions in pressure at one end of the aeration system (Fig. 1a). Wind blowing across tall, dead, broken culms generates pressures lower than atmospheric due to the venturi effect, and air enters the plant via shorter, broken culms exposed to lower wind speeds (Armstrong J *et al.* 1992, 1996c). The venturi effect of wind blowing across an open cylinder is described by Bernoulli's equation: $\Delta P = -\frac{1}{2} \rho V^2$; where ΔP is the pressure differential developed (Pa), ρ is the density of air (kg m^{-3}), and V is the wind velocity (m s^{-1}) (Armstrong J *et al.* 1992). Through-flows are determined by ΔP and internal resistance to flow; wider culms have lower internal resistance than narrow culms (Armstrong J *et al.* 1992). Static ΔP due to the venturi effect was about 60% of theoretical values, presumably due to the culms being leaky (via fractures, abscised buds, insect damage) and having somewhat jagged rims (Armstrong J *et al.* 1992). Venturi-induced flows may ventilate the submerged stems and rhizomes at times when flows due to positive pressures in living tissues would be low, such as during winter when leaf sheaths die and/or at night when air humidity is high (Armstrong J *et al.* 1992). Whether venturi-induced flows also occur in other emergent wetland species remains to be determined.

Flows arising from positive pressures generated in living shoot tissues

The mechanism by which a gradient in water vapour concentration ($\Delta[\text{H}_2\text{O}_{(g)}]$) across a microporous partition results in pressurization and through-flow of gases has been explained in detail elsewhere (Dacey 1981; Armstrong *et al.* 1996a, b). In brief, the phenomenon requires: (i) humid air enclosed in a chamber, the surface of which has pores within the size range (see below) to offer significantly more resistance to pressure flow than to diffusion of gas molecules ('Knudsen regime'; Leuning 1983); (ii) the chamber must be surrounded by a much larger volume of air that is less humid than that in the chamber; and (iii) a continuous supply of water must be available to maintain the humidity in the chamber, because some water will be lost to the surrounding air. Since $\text{H}_2\text{O}_{(g)}$ occupies space in the chamber it

dilutes the concentrations of other atmospheric gases, resulting in concentration gradients of N_2 and O_2 into the leaf, so these gases diffuse in, and increase the total pressure within the chamber. The static pressure (i.e. without flow) reached in an ideal system is described by the equation: $\Delta P = (P_a + P_{wi} - P_{wa}) - P_a$; where ΔP is the static pressure differential developed, P_a is pressure of the atmosphere, P_{wi} is water vapour pressure inside the chamber, and P_{wa} is water vapour pressure of the atmosphere outside the chamber (all units in Pa) (Armstrong *et al.* 1996a). Pressurization can occur with pores up to $3 \mu\text{m}$ in diameter, depending on other factors, such as temperature, overall porosity of the partition, and thickness (i.e. diffusion path length), but static pressures increase as pore size decreases (Leuning 1983; Armstrong *et al.* 1996a, b). If the chamber has an outlet, then pressurization will result in a flow of gases via the outlet at a rate determined by the pressure gradient and resistance to flow, with the dynamic pressure (i.e. with flow) being lower than the static pressure. The influences of pore size in the partition, humidity gradients, and other factors on pressurization and flow rates have been considered in mathematical models and elegantly demonstrated using experimental systems (Armstrong J & Armstrong 1994; Armstrong *et al.* 1996a, b). For a given resistance in the exit pathway, maximum flow rates occur when the diameters of the pores in the surface of the chamber are $\sim 0.2 \mu\text{m}$ (Armstrong J & Armstrong 1994; Armstrong *et al.* 1996a). Pressures and flows generated via this mechanism in the lacunae of plants have been termed 'humidity-induced pressurization' and 'humidity-induced convection', respectively, in much of the botanical literature. The terms $\Delta[\text{H}_2\text{O}_{(g)}]$ -induced pressurization and $\Delta[\text{H}_2\text{O}_{(g)}]$ -induced through-flow are used in the present report.

The morphology and location of the microporous partition has been studied in only a few species. In *Phragmites australis*, the stomates in the sheaths and culm nodes may function as the microporous partition, with the narrowest constriction ($0.13\text{--}0.25 \mu\text{m}$) within the stomatal pore (Armstrong J & Armstrong 1991). In contrast, stomatal apertures in *Spartina alterniflora* are much larger ($2 \mu\text{m} \times 10 \mu\text{m}$); so, the 'partition' in this species may result from the combined resistances to gas flow across the leaf mesophyll and the stomates (Hwang & Morris 1991). Tortuous intercellular paths (diameter $\sim 1.5\text{--}2 \mu\text{m}$ and lengths $\sim 70 \mu\text{m}$) through the chlorenchyma in the sheaths were also noted as being of possible significance to pressurization in *Phragmites australis* (Armstrong J & Armstrong 1991). In *Nuphar luteum*,

one of the few floating-leaved species examined to date, stomatal apertures were also considered too large ($1\ \mu\text{m} \times 3\ \mu\text{m}$ in young leaves, Dacey 1981; $2.4\ \mu\text{m} \times 5.6\ \mu\text{m}$ in leaves of undefined age, Schroder *et al.* 1986) to support Knudsen-diffusion. However, in contrast to the conclusion of Dacey (1981), pores of $1\ \mu\text{m} \times 3\ \mu\text{m}$ can support, at least some, pressurization under certain conditions (Leuning 1983; Armstrong J & Armstrong 1994; Armstrong *et al.* 1996a). Nevertheless, pores of a suitable size ($\sim 0.1\ \mu\text{m}$) were present in a monolayer of cells between palisade and spongy parenchyma *within* the leaf (Dacey 1980; Schroder *et al.* 1986). The microporous partition was also suggested to reside *within* the leaves of *Nelumbo nucifera* (Mevi-Schutz & Grosse 1988a, b). However, an effective pore size of $0.03\ \mu\text{m}$ was estimated experimentally, which was much smaller than the size inferred from anatomical studies (Dacey 1987). Clearly, further research is needed on the anatomical and morphological features that enable pressurization in leaf tissues of wetland plants.

Leaf temperature can have a marked effect on pressurization and resulting through-flows, particularly in floating-leaved plants (Dacey 1981; Schroder *et al.* 1986). For example, leaves of *Nuphar luteum* are warmed by the sun's radiation (Dacey 1981), or at night from conduction of heat to the leaves from lake water that is warmer than the night air (Dacey & Klug 1982b). Temperature gradients (leaf warmer than surrounding air) could enhance pressurization via two mechanisms: (i) increased $\Delta[\text{H}_2\text{O}_{(\text{g})}]$; and/or (ii) 'thermal diffusion' (defined below) (e.g. Dacey 1981; Schroder *et al.* 1986; Große 1996a; Armstrong *et al.* 1996b). For conditions most relevant to leaves of emergent wetland species, mathematical modelling indicates pressurization resulting from $\Delta[\text{H}_2\text{O}_{(\text{g})}]$ (due to differences in humidity *per se*, and via effects of leaf-to-air temperature gradients) as the dominant mechanism where the microporous partition exists between the drier atmosphere and humid interior of leaves/sheaths (Steinberg 1996). In the case of floating-leaves, for which the microporous partition may be internal, mathematical modelling has been impeded by a lack of data describing the conditions across the postulated partition *within* the leaf; such measurements pose a technical challenge.

Increased $\Delta[\text{H}_2\text{O}_{(\text{g})}]$ resulting from gradients in temperature

Air in turgid leaves is near $\text{H}_2\text{O}_{(\text{g})}$ saturation (Ward & Bunce 1986), but the concentration of $\text{H}_2\text{O}_{(\text{g})}$ in air at any particular relative humidity increases markedly as temperature rises (Jones 1992). Therefore, a gradient in leaf-to-air temperature (leaf warmer) results in a higher leaf-to-air $\Delta[\text{H}_2\text{O}_{(\text{g})}]$, increasing the diffusion of N_2 and O_2 into the leaf and thus pressurization (Steinberg 1996; Armstrong *et al.* 1996b). The temperature-enhanced pressurization via this mechanism involving $\Delta[\text{H}_2\text{O}_{(\text{g})}]$ is *not* the same as the mechanism of pressurization referred to by physicists as 'thermal diffusion' (or 'thermal osmosis'), the later phenomenon does *not* involve $\Delta[\text{H}_2\text{O}_{(\text{g})}]$ and is discussed below.

'Thermal diffusion'

The terms and physical theory for 'thermal diffusion' have been discussed in detail elsewhere (Armstrong *et al.* 1991, 1996b; Große 1996a). In brief, the theory and experimental work by physicists were developed using a pure gas in a two-chamber system separated by a microporous partition; a temperature gradient across the partition results in an increased pressure on the warmer side (Große 1996a and references therein). If the pores in the partition are $\ll 0.1\ \mu\text{m}$, then $\Delta P = P_a(T_i/T_a)^{1/2} - P_a$; where ΔP is the static pressure differential developed, P_a is pressure of the atmosphere, T_i is temperature of air inside the chamber, and T_a is temperature of air outside the chamber (pressure in Pa, temperature in °K) (Armstrong *et al.* 1996b). Model experimental systems consisting of a chamber (with an outlet) containing, and surrounded by, dry air, have been developed in an attempt to represent the situation in plants (Armstrong J & Armstrong 1994; Armstrong *et al.* 1996b; Dedes & Woermann 1996). Dry air was used to avoid pressurization resulting from gradients in temperature acting via enhanced $\Delta[\text{H}_2\text{O}_{(\text{g})}]$. Static pressures developed in response to temperature gradients in one of the experimental models were close to theoretical values (Dedes & Woermann 1996), whereas in the other the pressures and flows developed were very small (Armstrong J & Armstrong 1994).

'Thermal diffusion' has been suggested as the major mechanism of pressurization in some floating-leaved species (Große & Bauch 1991), despite the caution of some authors (Dacey 1981; Armstrong *et al.* 1991; Steinberg 1996). Elucidation of the role of 'thermal diffusion' in generating pressures above atmospheric in plant tissues has been difficult because the processes of $\Delta[\text{H}_2\text{O}_{(\text{g})}]$ - and 'thermal diffusion'-pressurization are essentially impossible to separate experimentally in the multicomponent gas mixture typical of leaves and the atmosphere (Dacey 1981; Armstrong *et al.* 1996a, b). For example, although Mevi-Schutz & Grosse (1988a) claimed to have evaluated the effect on pressurization of temperature, independent of $\Delta[\text{H}_2\text{O}_{(\text{g})}]$, by using air-dried leaves of *Nelumbo nucifera*; the flows were two orders of magnitude lower than in 'fresh' leaves, and the results are equivocal because both the leaves and air would have contained some H_2O , depending on humidity in the laboratory.

Pressurization in floating-leaves has been suggested to result from temperature gradients (and therefore also $\Delta[\text{H}_2\text{O}_{(\text{g})}]$) *within* the leaf. The lower tissues in the leaf being relatively warmer due to: (i) cooling of the more peripheral tissues during transpiration in the day time (suggested by Grosse *et al.* 1991; Schroder *et al.* 1986; Armstrong *et al.* 1996b); or (ii) contact with lake waters warmer than the air just above the surface in the night time (Dacey & Klug 1982b). However, when considering experimental results from floating-leaved species, gradients in temperature (and therefore also $\Delta[\text{H}_2\text{O}_{(\text{g})}]$) between the external air and the gas in the leaves are usually discussed, even by those authors advocating the location of the microporous parti-

tion *within* the leaves. This seems imprecise, and presumably contributes to the situation noted by Steinberg (1996) that values of static pressures given in the literature for floating-leaved species tended to be only 5–30% of poten-

tial pressures, when calculated using data on leaf-to-air gradients; a fact Steinberg (1996) ascribed to leaves being 'leaky' to Poiseuille outflow.