Changes in growth, porosity, and radial oxygen loss from adventitious roots of selected mono- and dicotyledonous wetland species with contrasting types of aerenchyma

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ABSTRACT

Growth in stagnant, oxygen-deficient nutrient solution increased porosity in adventitious roots of two monocotyledonous (Carex acuta and Juncus effusus) and three dicotyledonous species (Caltha palustris, Ranunculus sceleratus and Rumex palustris) wetland species from 10 to 30% under aerated conditions to 20–45%. The spatial patterns of radial oxygen loss (ROL), determined with root-sleeving oxygen electrodes, indicated a strong constitutive ‘barrier’ to ROL in the basal root zones of the two monocotyledonous species. In contrast, roots of the dicotyledonous species showed no significant ‘barrier’ to ROL when grown in aerated solution, and only a partial ‘barrier’ when grown in stagnant conditions. This partial ‘barrier’ was strongest in C. palustris, so that ROL from basal zones of roots of R. sceleratus and R. palustris was substantial when compared to the monocotyledonous species. ROL from the basal zones would decrease longitudinal diffusion of oxygen to the root apex, and therefore limit the maximum penetration depth of these roots into anaerobic soil. Further studies of a larger number of dicotyledonous wetland species from a range of substrates are required to elucidate the ecophysiological consequences of developing a partial, rather than a strong, ‘barrier’ to ROL.

Key-words: Caltha palustris L.; Carex acuta L.; Juncus effusus L.; Ranunculus sceleratus L.; Rumex palustris Sm.; aerenchyma; soil flooding; radial oxygen loss; root growth.

INTRODUCTION

Wetland plants are challenged by several stresses associated with periodic or permanent flooding of their habitat (Blom 1999). One important stress in wetland habitats is the rapid depletion of soil oxygen following the onset of flooding due to the much slower rates of diffusion in the liquid compared to the gas phase (Jackson & Drew 1984; Drew 1997). The resulting oxygen deficiency in the roots of non-adapted species is considered to be the primary cause of waterlogging damage (Trought & Drew 1980). Wetland or semi-aquatic species, however, have adapted to these conditions by either rooting superficially in order to take advantage of the oxygen available in the upper soil layers (see references in Jackson & Drew 1984), or by developing extensive aerenchyma in the roots (Armstrong 1979; Justin & Armstrong 1987; Laan et al. 1989a; Visser, Blom & Voesenek 1996a).

Aerenchyma provide a low-resistance internal pathway for the exchange of gases between the plant parts above the water and the submerged tissues; for example oxygen diffusion from the shoots to the roots (Armstrong 1972; Armstrong 1979; Laan et al. 1990) and the venting of root- and soil-derived gases such as ethylene (Visser et al. 1997) and methane (Butterbach-Bahl, Papen & Rennenberg 1997) from the roots to the atmosphere. Consumption of oxygen by tissues along the diffusion path in aerenchymatous roots will decrease the concentration of oxygen available at the root apex, eventually restricting the final length the root attains (Armstrong 1979; Armstrong et al. 1991). A potentially greater sink for oxygen in the aerenchyma may be radial loss to the soil and consumption in the rhizosphere by micro-organisms or by the oxidation of reduced chemicals. Many wetland species prevent excessive oxygen loss from the basal root zones by forming roots with a complete or partial ‘barrier’ to radial oxygen loss (ROL) in their epidermis, exodermis or subepidermal layers (Armstrong 1979; Jackson & Drew 1984; Armstrong & Armstrong 1988; Jackson & Armstrong 1999).

The majority of studies concerning ROL have examined monocotyledonous species, since these are either dominant in many wetland systems, for example, Phragmites (Armstrong et al. 1996), Glyceria (Bodelier et al. 1998), Juncus (Hacker & Bertness 1995; Sorrell 1999) and Carex (Moog & Brüggemann 1998) or important crops such as Oryza sativa (Armstrong 1971; Kludze, DeLaune & Patrick 1993; Colmer et al. 1998). These studies have contributed
greatly to the understanding of root adaptations to water-logged soils, but nevertheless the focus on monocotyledonous species that all form lysigenous aerenchyma (Justin & Armstrong 1987; Koncalová 1990) means that knowledge on oxygen movement in roots of dicotyledonous species that undergo secondary growth and in several cases form schizogenous aerenchyma is scanty. Interestingly, the data of Laan et al. (1989b) for ROL along roots of two schizogenous aerenchyma forming wetland species of the dicotyledonous genus Rumex show that the basal root zones were relatively permeable to oxygen loss when compared to roots of wetland monocotyledonous species. Nevertheless, the flatness of ROL profiles from root apex to base indicates a partial barrier to ROL in the basal zones, so that oxygen loss is less significant than in intolerant species such as Pismum sativum (Healy & Armstrong 1972), Triticum aestivum (Thomson et al. 1992) and Brassica napus (Voesenek et al. 1999). The high rates of ROL from the basal root zones of these dryland crops, in combination with low root porosity, probably contributes to their intolerance to soil flooding (Jackson & Drew 1984).

The general aim of the experiments described in the present article was to evaluate the porosity and spatial patterns of ROL for adventitious roots of two monocotyledonous and three dicotyledonous wetland species. The species were selected based on preliminary observations of contrasting types of aerenchyma.

More specifically, we addressed the following questions:

1. How does the morphology of adventitious roots of wetland species with a constitutively high root porosity respond to oxygen-deficient conditions?
2. Can only monocotyledonous wetland species form a strong ‘barrier’ against ROL in their adventitious roots?
3. Is there a relationship between the presence of a complete or partial ‘barrier’ against ROL and the type of aerenchyma in the root?

MATERIALS AND METHODS

Plant materials and culture

Five plant species that are common in many European river systems were selected for this study due to the ability of these plants to grow under soil-flooded conditions and to form adventitious roots with contrasting types of aerenchyma. Two monocotyledonous species were chosen, namely (i) Carex acuta L., which occurs along ponds and in sedge marshes, and (ii) Juncus effusus L., growing on open, moist to wet soil; and three dicotyledonous species were examined, namely, (i) Caltha palustris L., a species from reedland, wet grasslands and springs, (ii) Ranunculus sceleratus L. and (iii) Rumex palustris Sm., the latter two from nutrient-rich mudflats.

Young plants of C. palustris, C. acuta and J. effusus were collected from the field. R. sceleratus and R. palustris were raised from seed (see Rijnders et al. 1996) on nutrient solution. After transfer to hydroponics, all species were grown for several weeks in a regularly refreshed, aerated nutrient solution in a temperature-controlled room at 22 °C as described in Visser et al. (1996b).

Oxygen treatments

At least 2 weeks before measurements started, plants of each species were either transferred to containers with (a) stagnant nutrient solution containing 0·1% [w/v] agar that had previously been flushed overnight with N₂ gas to remove dissolved oxygen (before being left stagnant), or (b) fresh, aerated nutrient solution. Oxygen concentrations in the bulk solution are generally between 0·4 and 1·0 g m⁻³ for the stagnant 0·1% agar solutions (Visser et al. 1996b). These solutions were renewed weekly.

Root extension, diameter and porosity

Rates of extension of roots initially 5–15 cm in length were determined by marking selected roots with a xylene-free felt-tip pen or by dipping the roots in a solution of 0·15% [w/v] neutral red in water for a few seconds. The initial lengths were measured using a ruler and then re-measured 3 d later so that the extension rate of each root was calculated. The method of marking roots did not significantly affect root extension (data not shown).

The root diameter at various distances behind the root apex was measured using an Olympus BX-40 microscope with calibrated eyepiece reticle.

Porosity of the adventitious roots was determined after the method of Raskin (1983), using the equations as modified by Thomson et al. (1990). The apical 8 cm of 10–50 roots were detached with a razor blade and cut into segments of approximately 1·5 cm. The fresh weight of the sample was determined after carefully blotting with tissue paper to remove surface water. Buoyancy of root samples before and after being vacuum infiltrated with water was measured using a balance with a water-filled flask containing the root samples attached to the under-carriage and submerged in a beaker of water under the balance. The porosity was calculated from the difference in weight of the segments before and after infiltration (volume of air space), divided by the difference between fresh weight and weight under water before infiltration (volume of the segments).

The distribution of porosity along the length of adventitious roots of R. palustris and C. acuta was also evaluated by measuring the porosity of root segments cut at 2, 4, 6 and 8 cm behind the apex.

Root anatomy

Fresh sections were cut with a MIC504 hand microtome (Euromex Microscopes BV, Arnhem, The Netherlands) at 5 cm behind the apex of roots after vacuum-infiltrating the roots with water. Sections were examined using an Olympus BX-40 microscope and photographed with an
Radial oxygen loss (ROL) from intact roots when in an oxygen-free medium

The loss of oxygen from intact roots when in an oxygen-free medium was quantified using root-sleeving oxygen electrodes following the method of Armstrong (1971) and Armstrong *et al.* (1994). Plants from the aerated and stagnant treatments were transferred into Perspex chambers of either 5 cm × 5 cm × 25 cm for small plants or 10 cm × 10 cm × 25 cm for larger plants, filled with a stagnant, deoxygenated solution containing 0·1% (w/v) agar, 5 mol m⁻³ KCl, and 0·5 mol m⁻³ CaSO₄. The shoot of each plant was held upright in air by the lid on the box, while the root system was completely submerged in the de-oxygenated stagnant medium with the root–shoot junction of the adventitious roots never more than 1·5 cm below the surface of the medium. Holes in the lid were sealed with Terostat sealing profile (Henkel Teroson, Heidelberg, Gemary). Light intensity and temperature were 200 μmol m⁻² s⁻¹ PPFD (photosynthetic photon flux density) and 23 °C, respectively. Two hours after being transferred to the chambers, a cylindrical platinum oxygen electrode (internal diameter either 2·25 or 3·75 mm, depending on root diameters; height 5 mm) was positioned around an adventitious root (length 10–16 cm) and the centre of the electrode was initially at 8·0 cm behind the apex. After the reading of the ‘diffusion current’ generated by the reduction of oxygen at the polarized platinum surface of the root-sleeving electrode stabilized, the value was recorded and the electrode was shifted to positions (centre of the electrode) at 5·0, 3·0, 2·0, 1·0 and 0·5 cm behind the root apex, and readings were taken. Five to six replicate roots from at least three plants were measured for each species and treatment.

Statistical analyses of data

Differences in root extension rates, root diameters and root porosity between treatments were analysed with a Student *t*-test or, when the data were not normally distributed, with a Mann–Whitney rank sum test.

RESULTS

Growth, morphology and anatomy of adventitious roots in the five wetland species change when exposed to stagnant conditions

Formation of new adventitious roots continued in all five species when plants were transferred to stagnant deoxygenated 0·1% agar nutrient solution. The extension rate of these roots, however, decreased in three of the species (Fig. 1), with the largest decline of about 60% in *Ranunculus sceleratus*. Extension rates of adventitious roots of *Rumex palustris* and *Juncus effusus* were not significantly affected by the stagnant treatment.

The stagnant treatment resulted in increased root diameters in three species, namely *R. palustris, J. effusus* and *Caltha palustris*, although the increase in diameter in the latter species was only small (Fig. 2). All species already had rather thick adventitious roots even under aerated conditions, with the diameter of the roots of *R. palustris* being thinnest at 0·7 mm.

Thick roots in wetland plant species are often associated with the formation of aerenchyma in the cortex. Indeed,
comparison of the root porosity for plants from the two treatments revealed substantial increases in the relative volume of air spaces in the roots grown in stagnant solution (Fig. 3). The relative increases were at least 40%, even for species with 25–30% porosity in aerated roots (viz. *J. effusus*, *R. palustris*), and two-fold in the species with only about 10% porosity for roots grown under aerated conditions (viz. *C. palustris*, *Carex acuta* and *R. sceleratus*).

The structures of the aerenchyma responsible for these increases in root porosity were diverse among the five species (Fig. 4). *C. acuta* and *J. effusus* developed extensive radial lacunae, that in *C. acuta* were intersected by cell wall residues in the same direction as the root circumference. In *C. palustris* and *R. sceleratus* schizogenous aerenchyma formed initially, only followed in later stages of root development by the appearance of larger, irregular lysigenous cavities. *R. palustris* was the only species that did not form lysigenous aerenchyma. The schizogenous aerenchyma in this species was arranged in a honeycomb-like structure. Typically, the epidermis and exodermis in *C. acuta* and *J. effusus*, and also the epidermal and subepidermal layers of *C. palustris*, consisted of three to six layers of densely packed cells with few intercellular spaces. In contrast, *R. sceleratus* and *R. palustris* showed no distinct exodermis and the outermost cells of the cortex were not differently arranged compared to the inner cortex.

Figure 5 shows that two of these different types of aerenchyma have an impact on the distribution of porosity along roots. Schizogenous aerenchyma in *R. palustris* resulted in a high porosity within 2 cm of the root apex, whereas lysigenous aerenchyma in *C. acuta* was only fully developed at 4 cm behind the root apex.

Profiles of radial oxygen loss along adventitious roots differ among the five species

The different anatomical characteristics of the roots may affect the resistance within the root to longitudinal oxygen diffusion, and also to radial oxygen loss from the aerenchyma to the rhizosphere. Therefore, radial oxygen loss (ROL) was measured at various distances behind the root apex in order to assess oxygen supply to the apical region as well as patterns of resistance to ROL along the roots.

The profiles of ROL differed considerably among the five species (Fig. 6). Rates of ROL from roots of aerated *C. palustris* plants were highest in the basal regions of the roots and declined slightly towards the root tip. In contrast, roots of this species grown in the deoxygenated stagnant solution showed highest ROL near the apex and it declined in the more basal regions. This response suggests that the permeability of the exterior of the root to oxygen declined for plants grown in stagnant solution, a feature that has been termed a ‘barrier to ROL’ in the literature. Both aerated and stagnant roots of *C. acuta* and *J. effusus* exhibited a strong ‘barrier’ to ROL in the basal zones, as very little oxygen leakage was detected in the older regions, whereas close to the root apex the loss of oxygen increased. ROL near the apex of roots of *J. effusus* increased remarkably, whereas for *C. acuta* ROL near the apex was still substantially higher than at the basal zones but only 10–20% of that of *J. effusus*. ROL patterns along either the aerated or the stagnant roots of *R. palustris* and *R. sceleratus* were similar. For roots of aerated plants of these two species, ROL decreased as the electrode was positioned closer to the root apex (further from the root/shoot junction), a pattern of ROL similar to roots of *C. palustris* raised in aerated solution. In contrast, roots of plants of *R. palustris* and *R. sceleratus* raised in stagnant solution showed relatively equal ROL along the entire apical 8 cm; that is, values measured towards the apex of these roots did not decline substantially when compared with ROL at the most basal position tested.

Given the relatively high rates of ROL from the basal regions of *R. palustris* roots grown in the deoxygenated stagnant solution, the ROL from plants of the same species raised in pots containing a waterlogged soil/clay mixture was also checked. The growth procedure was as described by Voesenek & Blom (1989). Plants were raised under drained conditions for 5 weeks and then waterlogged to 2 cm above the soil surface for 1 week. Plants were carefully washed from the soil, and patterns of ROL from adventitious roots (8–10 cm in length) were determined. The pattern of ROL from roots of these soil-flooded plants was very similar to that of the same species when grown in stagnant solution. We also measured ROL from several adventitious roots of 28-day-old *Rumex maritimus* L. raised in stagnant solution for the final 2 weeks under the same conditions as described in the Materials and Methods for the five main species examined, and the pattern of ROL for
R. maritimus was similar to that of R. palustris (i.e. relatively high rates of ROL from basal regions when compared to monocotyledonous wetland species).

**DISCUSSION**

**Increased porosity facilitates internal oxygen diffusion in adventitious roots**

The wetland species studied in our experiments responded to oxygen-deficient conditions by increasing adventitious root porosity (Fig. 3) and in three of the five species root diameter (Fig. 2). These acclimations lower the resistance to longitudinal diffusion of gases in the roots, hence increasing internal aeration of the root system and enabling deeper root penetration into anaerobic soils (Armstrong 1979; Laan, Clement & Blom 1991). Moreover, increased root porosity and diameter would also enhance venting of potentially phytotoxic gases such as ethylene (Visser et al. 1997). The increases in porosity were above the relatively high constitutive levels in roots of these species under aerated conditions (Fig. 3). In an earlier report, Justin & Armstrong (1987) examined 91 wetland species and those with 10–20% porosity in roots under drained conditions mostly doubled or even tripled their volume of aerenchyma when waterlogged, as was found for Caltha palustris, Carex acuta and Ranunculus sceleratus in the present study. On the other hand, only three of the six species with a porosity of 30% or more under drained conditions increased further in root porosity upon soil flooding. In the present study, aerated adventitious roots of both Rumex palustris and Juncus effusus had a high porosity (25–30%) and this

increased to about 45% for plants grown in stagnant solution (Fig. 3). The clear increase in root porosity of *J. effusus* in the present study contrasts with the findings of Justin & Armstrong (1987), who found an adventitious root porosity for this same species of about 40% under both drained and flooded soil conditions. These contrasting results may be due to differences in the tissues sampled in the two studies. In the present work the porosity of the apical 8 cm of roots, which can contain a relatively large proportion of tissues in which the aerenchyma are not yet fully developed, was determined, whereas Justin & Armstrong (1987) sampled the entire root system with roots as long as 30 cm, so that the apical tissues of lower porosity would not have had a large influence on the final values. Comparison of the results from these two studies suggests that the few centimetres of apical roots are the most responsive in terms of changes in root porosity upon soil flooding.

The type of aerenchyma formed can also influence the porosity just behind the root tip. Species with schizogenous aerenchyma, such as *R. palustris*, attain a high porosity within 0·5–1 cm behind the root apex (Fig. 5; other *Rumex* species see Laan et al. 1989a), whereas in roots with lysigenous aerenchyma the porosity increases for a considerable length behind the tip (viz 2–6 cm), as shown for *C. acuta* in the present study (Fig. 5), *Phragmites australis* (Armstrong et al. 1996), *Oryza sativa* (Armstrong 1971) and *Triticum aestivum* (Thomson et al. 1992). The functional significance of having one or the other type of aerenchyma has not been fully evaluated, but the larger volume of gas spaces closer to the tip of roots with schizogenous aerenchyma should enhance oxygen supply to the apex.

**Figure 5.** Distribution of porosity along adventitious roots of *Carex acuta* (●) and *Rumex palustris* (▲), grown in stagnant, deoxygenated nutrient solution containing 0·1% agar for at least 2 weeks. Porosity was measured for segments taken at 0–2, 2–4, 4–6 and 6–8 cm from behind the root apex (three replicates; error bars indicate SEs).

**Figure 6.** Radial oxygen loss (ROL) from adventitious roots of intact plants of five wetland species, grown in either aerated nutrient solution (●) or for at least 2 weeks in stagnant, deoxygenated solution containing 0·1% agar (○). (a) *Caltha palustris*. (b) *Carex acuta*. (c) *Juncus effusus*. (d) *Ranunculus sceleratus*. (e) *Rumex palustris*. ROL from roots in an oxygen-free medium was measured with the centre of the cylindrical electrode positioned at 0·5, 1, 2, 3, 5 and 8 cm behind the root apex. Intact plants had shoots in air and roots enclosed in a perspex chamber containing the medium. Root lengths were between 10 and 16 cm (five to six replicates; error bars indicate SEs).
Exodermal and subepidermal cell layers can impede radial oxygen loss from adventitious roots in some wetland species

Adventitious roots of *Car. acuta* and *J. effusus* contained layers of cells densely packed in a hexagonal configuration on the external side of the cortex (Fig. 4B & C). The walls of these cells in *C. acuta* showed additional secondary thickening and microscopy using violet light revealed strong epifluorescence of these exodermal layers, indicating a possible deposition of lignin or suberin (data not shown). It is therefore not surprising that rates of ROL from the basal root zones of these two monocotyledonous species were very low (Fig. 6b & c). Suberin and lignin deposits are commonly found in roots of wetland species, and may function as the ‘barrier’ that impedes the radial diffusion of oxygen to the rhizosphere (Clark & Harris 1981; Gaynard & Armstrong 1987; Armstrong & Armstrong 1988; Jackson & Armstrong 1999). In adventitious roots of *C. acuta* and *J. effusus* examined in the present study, and also in *Juncus kraussii* (Inglis and Colmer, unpublished results), the ‘barrier’ to ROL was present in plants grown under aerated or stagnant conditions.

In a recent report, however, Colmer et al. (1998) demonstrated that in rice the ‘barrier’ to ROL was induced by growth in stagnant conditions. Our measurements for the dicotyledonous species *C. palustris* showed that this species also contains an inducible ‘barrier’ to ROL. Roots of *C. palustris* grown under aerated conditions leaked oxygen at relatively high rates along the entire length when placed in an oxygen-free medium (Fig. 6a, open symbols), whereas for roots developed under stagnant conditions ROL decreased markedly in the older regions but was maintained near the tip (Fig. 6a, closed symbols) indicating a reduction in the permeability to oxygen in the basal zones of these roots. An inducible ‘barrier’ to ROL may be advantageous for species that inhabit areas with infrequent and transient soil flooding (Colmer et al. 1998); however, *C. palustris* mostly inhabits areas with prolonged flooding so the adaptive significance of the inducible, rather than a constitutive ‘barrier’ to ROL in this species remains to be elucidated.

The rates of ROL just behind the apex of roots of *C. acuta* (Fig. 6) were relatively low in comparison with the two other species with root porosity of approximately equal values, namely *C. palustris* and *R. palustris* (Fig. 3). Possible reasons for this phenomenon may be a lower internal oxygen concentration in the aerenchyma and/or a higher resistance to ROL near the tip of roots of *C. acuta*. Further experiments utilizing microelectrodes to measure internal oxygen concentrations and ROL measurements at a higher spatial resolution are required to resolve these possibilities.

**Not all wetland species have a strong ‘barrier’ to radial oxygen loss**

Roots of both *R. sceleratus* and *R. palustris* showed substantial rates of ROL from the basal zones when compared to the monocotyledonous species (Fig. 6). We also checked the ROL patterns of roots of *R. palustris* grown in water-logged soil and for *Rumex maritimus* grown in stagnant solution; in both cases ROL patterns were similar to those shown for *R. palustris* in Fig. 6. The rather flat profiles of ROL from roots of *Rumex* suggest a ‘partial barrier’ to ROL (Laan et al. 1989b) since if the permeability of the root exterior was equal along the length then a steep increase in ROL would be expected as the electrode was positioned closer to the root/shoot junction due to the progressively higher internal oxygen concentrations towards the source along this diffusion gradient. An increase in epifluorescence of the cell walls surrounding the outermost schizogenous air spaces in stagnant *R. palustris* roots (data not shown), indicates that lignin and/or suberin may contribute to the lower radial permeability in the exterior of the roots from plants grown in stagnant solution. The high and even distribution of porosity to within 1 cm of the root apex (Fig. 5) could also contribute to the rather even rates of ROL along the axes of the *Rumex* adventitious roots. However, unlike Laan et al. (1989b) we did not observe any increases in ROL towards the tip of roots of *R. palustris* (soil or solution culture) and *R. maritimus* (6 replicate roots; data not shown).

The ‘partial barrier’ to ROL in adventitious roots of *R. palustris*, when compared with wetland monocotyledonous species with a ‘strong barrier’ to ROL, would result in a greater proportion of the internal oxygen supply being lost in a radial direction to the soil and therefore a shorter potential maximum length of root penetration into anaerobic soil. Roots of wetland plant species (e.g. *Littorella, Luronium* and *Isoetes*) from sandy substrates, which are low in organic matter, that do not become highly reduced in redox potential when flooded, have large aerenchyma cavities but also appear to be relatively permeable to ROL (Smits et al. 1990). The ecological advantage of not forming a ‘strong barrier’ to ROL may be prolonged uptake of water and nutrients by the basal root zones (Colmer & Bloom 1998). In addition, nitrifying micro-organisms (Both, Gerards & Laanbroek 1992) and even other plant species (Hacker & Bertness 1995) may benefit from high ROL along the root. Adventitious roots of the seagrass *Halophila ovalis* form schizogenous aerenchyma and this monocotyledonous species has a ‘strong barrier’ to ROL (Connell, Colmer & Walker 1999), showing this combination of aerenchyma type and a ‘strong barrier’ can occur in nature.

**CONCLUSIONS**

1 Wetland plant species that have constitutive aerenchyma in their root system are capable of further increases in root porosity when exposed to stagnant, oxygen-deficient conditions. Furthermore, in some cases the root diameter can increase, supporting a larger cross-sectional area of internal air spaces.

2 Both mono- and dicotyledonous wetland species may form a ‘barrier’ to prevent excessive ROL from the basal
root zones. This ‘barrier’ was induced by stagnant conditions in at least one dicotyledonous species (viz. *Caltha palustris*).

3 The two monocotyledonous wetland species studied, plus others examined in earlier work (e.g. *Oryza sativa*, *Phragmites australis*; Armstrong 1971; Armstrong & Armstrong 1988; Colmer et al. 1998) exhibited a ‘strong barrier’ to ROL, whereas in the dicotyledonous wetland species only a ‘partial barrier’ to ROL was present. ROL profiles of adventitious roots of these plants tended to be flatter from the apex to basal root zones for the plants grown in stagnant solution, suggesting a reduction in the radial permeability to oxygen of the root exterior. This treatment effect was substantial in *C. palustris* and much less marked in *Ranunculus sceleratus* and *Rumex palustris*. Further studies of a larger number of dicotyledonous wetland species from a range of substrate types are required to elucidate the ecophysiological consequences of developing a ‘partial’, rather than a ‘strong’, barrier to ROL.

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