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Internal oxygen transport in *Rumex* species and its significance for respiration under hypoxic conditions

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Abstract

Rumex thyrsiflorus, *Rumex crispus* and *Rumex maritimus* show a differential flood-tolerance in the river ecosystem in the Netherlands. *R. thyrsiflorus* occurs at high-elevated habitats and is flood-intolerant, the other two species occur at lower-elevated habitats and are flood-tolerant. We compared their respiratory activity under aerobic and anaerobic conditions in the root environment and quantified the internal gas transport. The results indicate that aerial oxygen can be used for root respiration in both aerobically and anaerobically grown plants. The amount of oxygen used via internal aeration increased with decreasing oxygen concentration in the root environment. Aerobically grown plants of *R. maritimus* and *R. crispus* already showed a high internal aeration, but there was a significant increase in internal oxygen transport in anaerobic plants, where new, aerenchymatous roots had formed. This indicates the functional significance of new root formation for respiration in these species upon hypoxia. After two weeks of anaerobiosis, more than 50% of the total respiration of the roots of young plants of *R. maritumus* and 40% of roots of young plants of *R. crispus* was due to internal aeration at low oxygen concentrations in the root environment.

In *R. maritimus* both young and old plants performed in this way, in *R. crispus* only young plants, while *R. thyrsiflorus* showed some internal aeration, but this was hardly detectable. These differences can be explained on the basis of a different morphology and concomitant diffusive resistance of both root and shoot system.

In experiments with different submergence levels of the shoot, the amount of internal aeration was positively correlated to the total leaf area protruding above the water surface in *R. maritimus*. This indicates a functional significance of the petiole and leaf elongation response upon total submergence of this species.

Introduction

Upon exposure to anaerobic conditions, many plant species form aerenchyma in their roots (Arber, 1920; Armstrong, 1979; Jackson and Drew, 1984; Justin and Armstrong, 1987; Konings and Verschuren, 1980; Laan *et al.*, 1989a). This response is supposed to be beneficial to plant growth or survival under situations of root inundation. Aerenchyma development increases root porosity, hence reduces the resistance to diffusive oxygen transport from shoot to root (Armstrong, 1979; Veen, 1989), so that aerobic respiration can be maintained in roots when the root environment becomes anoxic (Armstrong, 1979; Armstrong and Gaynard, 1976; Drew *et al.*, 1985; Lambers *et al.*, 1978; Prioul and Guyot, 1985).

Wheat plants can adapt to root anaerobiosis within a week by aerenchyma formation (Prioul and Guyot, 1985; Wiedenroth and Erdmann, 1989). Prioul and Guyot quantified the internal oxygen transport from the shoot to the root system

of anaerobically grown wheat plants. However, to allow internal aeration, the formation of an extended aerenchyma system is not strictly necessary. Armstrong *et al.* (1982; 1983) showed that pea roots with a porosity of only 2—4% showed internal aeration, and Armstrong (1979) and De Willigen and Van Noordwijk (1984) calculated that even effective porosities of about 1—4% can contribute significantly to root respiration under hypoxia in the root environment, provided that the gas-filled pores form a continuous system. Consequently, root respiration, measured as oxygen depletion from the root environment will be underestimated when additional oxygen is internally transported from the shoot to the root.

The aim of this study was to investigate the importance of internal gas transport for root respiration in three *Rumex* species, which occur in the river ecosystem in the Netherlands and show a differential response towards flooding (Laan *et al.*, 1989a;b). Their root system consists of a tap-root, from which laterals are formed. Upon flooding new laterals develop; the tolerant species *R. maritimus* and *R. crispus* both develop an aerenchyma system in the new lateral roots (Laan *et al.*, 1989a).

In the river ecosystem both *R. maritimus* and *R. crispus* are infrequently confronted with total submergence during the growth period of the plants (Van de Steeg, 1984; Voesenek *et al.*, 1989), a situation in which no efficient use can be made of the aerenchyma system. As a response both laminae and petioles elongate so that the water surface is reached (Voesenek and Blom, 1989). We investigated whether the functional significance of this elongation may be to serve as a base for the internal aeration of the root systems.

Materials and methods

Plant growth

Seeds of *Rumex thyrsiflorus* Fingerh., *R. crispus* L. and *R. maritimus* L. were collected from natural populations and sown on black polyethylene granules (stamylan LD, DSM, The Netherlands). After germination, which occurred within one week, the plants were separated into two batches.

One batch, used for the experiments with young plants, were allowed to grow on aerated hydroculture for 7 weeks (aerobically grown plants), with the following nutrient composition: Macronutrients: KNO_3 1 m*M*, $Ca(NO_3)_2$ 1 m*M*, $NaNO_3$ 1 m*M*, KH_2PO_4 0.5 m*M*, $MgSO_4$ 0.25 m*M*; Micronutrients: FeEDTA 0.25 m*M*, KCl 12.5 μM, H_3BO_3 6.3 μM, $MnSO_4 \cdot H_2O$ 0.5 μM, $ZnSO_4 \cdot 7H_2O$ 0.5 μM, $CuSO_4 \cdot 5H_2O$ 0.1 μM, H_2MoO_4 0.1 μM in a growth room (22°C; 16 h light at 200 μmol m^{-2} s^{-1} PAR, 8 h dark; R.H. 60%). Some of these plants were transferred to a stagnant, anaerobic (0.1% agar (w:v)) nutrient solution after 5 weeks and kept there for one to two weeks. In this period new laterals developed from the tap-root (anaerobically grown plants). All nutrient solutions were changed every two days and maintained at a constant pH of 5.5

Another batch (old plants) was allowed to grow for eight to ten weeks in a growth room (temperature 24°C; light intensity 500 μmol $\cdot$ $m^{-2} \cdot s^{-1}$ PAR for 16 h, 8 h dark; R.H. 70%); the nutrient solution was changed twice a week. Some of these plants were transferred to an anaerobic 0.1% agar in $\frac{1}{2}$ × full strength nutrient solution and both aerobic and anaerobic plants were allowed to grow for another one to two weeks in a growth chamber at the same light and temperature conditions. In this period the anaerobic plants developed a new lateral root system.

Experimental assembly

The experimental setup, used for the old plants, was derived from a measuring system used by Veen (1977) (Fig. 1a). A plant was placed in the system, with its roots in the root vessel (*RV*). Closed-cell rubber foam sealed the opening between the plant and the stopper at the upper side of the root vessel. Over the shoot of the plant a 'Perspex' cover (*K*) was mounted, through which air or nitrogen gas was blown. With a small rotary pump (*P*) (Eheim type 1018) a thermostatted (*C*) nutrient solution with a total volume of 3 liters was circulated at 1 L $\cdot$ min^{-1}. In the measuring chamber (*M*) a galvanic lead/silver electrode (Precision Scientific Inc.) was used to register the oxygen concentration. When the magnetic valve S_1 was opened and S_2 closed, the flow of water fell over a distance of about 10 cm into a vessel (*A*), which gave an adequate aeration of the nutrient solution. The

oxygen concentration at the start of each experiment varied depending on root size. When S_2 was opened and S_1 closed, the oxygen supply to the nutrient solution was prevented and uptake rate of oxygen by the plant roots was recorded at 5-min intervals using a HP 85 computer with a 3421A-data acquisition unit. From the depletion curve the relation between oxygen concentration and uptake was calculated.

The measuring system, used for the young plants (Fig. 1b), was comparable to the one used for the old plants. Instead of 3 liters, the net volume of the root vessel was 180 mL; a polarographic oxygen electrode according to Kimmich and Kreutzer (1969) was placed into the root vessel (*RV*) and optimal mixing of the nutrient solution was achieved by stirring with motor-driven paddle-boards (*ST*), together with the positioning of three vertical baffles at the inner side of the root vessel (*IB*). The shoot was separated from the root system by two crescent 'Perspex' lids, sealed with clay and lanolin. The shoot was covered with a 'Perspex' lid (*K*) and darkened by a black plastic cover (*B*); this 'Perspex' cover allowed the flow-through of air or nitrogen gas, or of water used to submerge the shoot to different levels. A thermostatic waterbath (*W*) (Hakke, type G-D8) contained 1 litre of the aforementioned nutrient solution (*NS*) plus 1% (w/v) glucose, which was aerated with a porous aeration-stone (*G*) and maintained at 25.0°C. After aeration for *ca.* 30 min, this nutrient solution was pumped into the inner root vessel (*RV*) with a peristaltic pump, and the vessel was closed. Oxygen consumption of the root system was calculated from a depletion curve, measured with an oxygen micro-sensor (Diamond Electro-Tech, Ann Arbor, Mich., USA). The nutrient solution was renewed after each measurement (*ca.* 50 min) to prevent a significant bacterial contribution to respiration. The first depletion curve was always made with air circulated through the shoot compartment, the second with a nitrogen gas flow. Changes from air to nitrogen gas were completed within one minute; depletion experiments could therefore be performed within 2 — 3 minutes. At the end of each set of measurements, the shoot was cut off and the remaining tap-root sealed with a mixture of clay and lanolin, after which the depletion of oxygen was measured.

The absolute zero oxygen point was checked

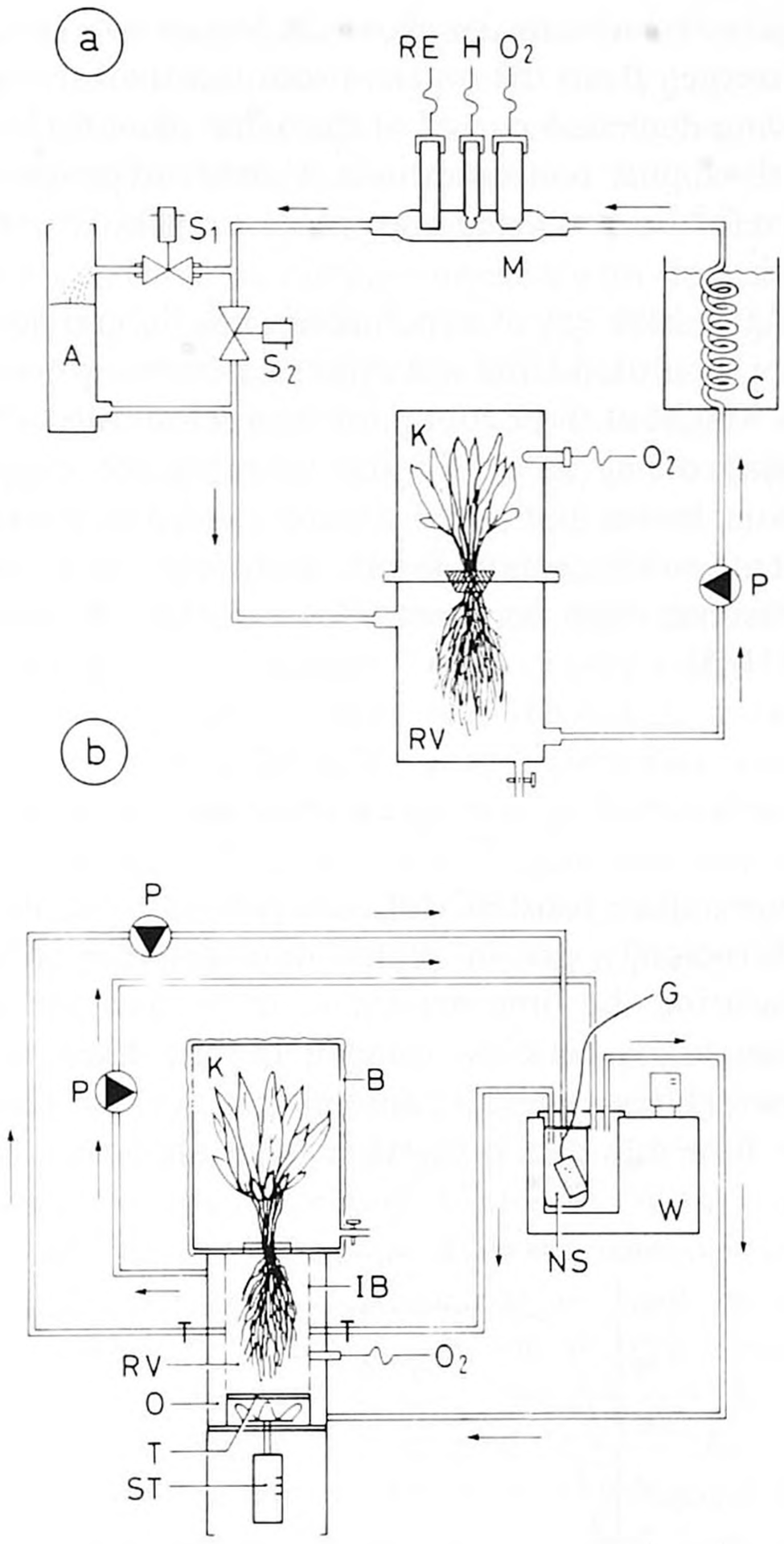

Fig. 1. Diagram of the measuring system for old plants **(a)** and for young plants **(b)**. RV = root vessel, K = perspex cover, P = pump, C = cooling bath, S = solenoid valve, A = aeration vessel, M = measuring chamber consisting of a reference electrode (RE), a pH electrode (H) and an oxygen electrode (O_2); B = black plastic cover, W = thermostatic waterbath, from which two flow-through systems are circulated: one via the inner root vessel (RV) and the other (cooling system) via the outer compartment (O), NS = nutrient solution, aerated by gas inlet (G), T = perforated table, ST = stirrer, IB = inner baffles to optimize mixing of the nutrient solution.

both by Winkler-titration and by measurement of nutrient solution, which was thoroughly bubbled with nitrogen gas.

To prevent the entry of photosynthetic oxygen, all experiments were performed in the dark. When starting the experiments immediately after the change from the light to the dark period, the first

depletion curve always showed a higher uptake rate of oxygen from the nutrient solution than the following depletion curves of the same plant, at least at the higher concentrations. Further experiments therefore were started after at least one hour in the dark.

After each set of experiments new lateral roots were separated from old ones and from tap-roots; dry weight of these root parts was determined after drying (48 h, 70°C). In the submergence experiments, leaves and petioles were severed at the different submergence levels and leaf area was measured with an area meter (MOP Kontron GMBH).

Determination of pore-space resistance

Pore-space resistance of 7-cm petiole segments of anaerobically grown plants was determined by measuring the time needed to move 4 cm^3 of air through the petioles, using a burette filled with water, giving a pressure difference of 5.5 kPa. From the flow-rate the pore-space resistance was calculated according to Armstrong (1979) and Armstrong *et al.* (1988).

Results

Oxygen uptake by Rumex root systems was independent of the oxygen concentration in the surrounding medium down to *ca.* 50 μM (Critical Oxygen Pressure for Respiration in the measuring system (=COPR), Fig. 2). Higher oxygen depletion rates were obtained with nitrogen gas than with air in the shoot compartment; oxygen uptake rates with nitrogen gas in the shoot compartment and those of decapitated plants were similar and represent the actual respiration rate of the root systems. Respiration depending on internal oxygen transport was calculated as the difference between oxygen depletion rates of roots of intact plants supplied with air in the shoot environment and that of decapitated plants, down to the COPR.

With young, aerobically grown plants of both *R. maritimus* and *R. crispus* (Fig. 2a,c), the oxygen

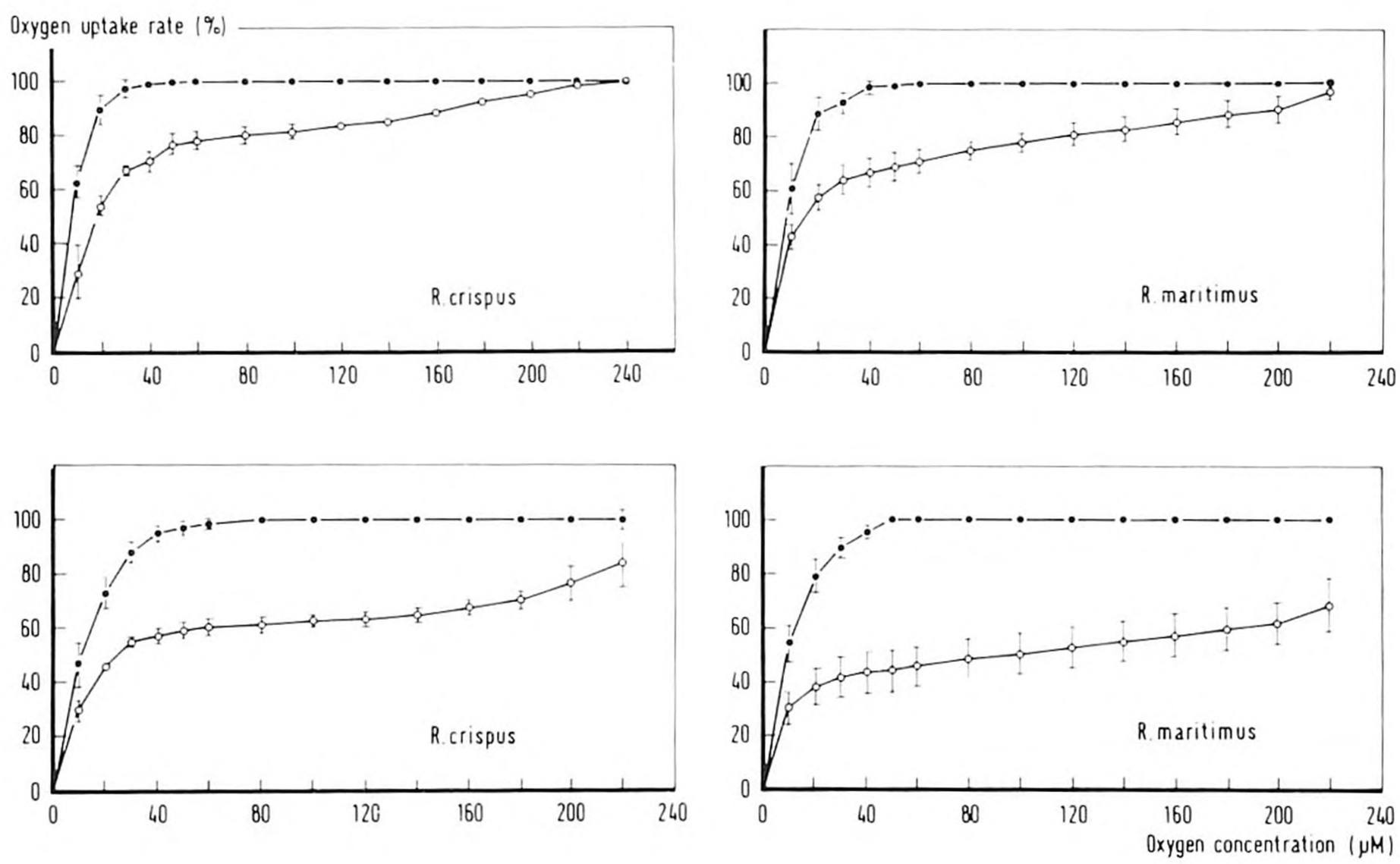

Fig. 2. Effect of air in the shoot compartment (○) or removal of the shoot (●) on the oxygen consumption from the root environment by root systems of *Rumex maritimus* and *R. crispus* plants, grown aerobically (*top*) or after 1—2 weeks anaerobiosis (*bottom*). (Data as a percentage of maximal respiration rate at 220 μM O_2 = 100%, being 192 ± 8 (aerobic *R. maritimus*), 192 ± 44 (anaerobic *R. maritimus*), 175 ± 54 (aerobic *R. crispus*) and 167 ± 13 (anaerobic *R. crispus*) μmol O_2 (g dry wt)$^{-1}$ hr^{-1}; means of 3—4 replicates ± SE; measurements performed after at least one hour in the dark; age of plants 5 weeks plus 1—2 weeks anaerobic treatment.

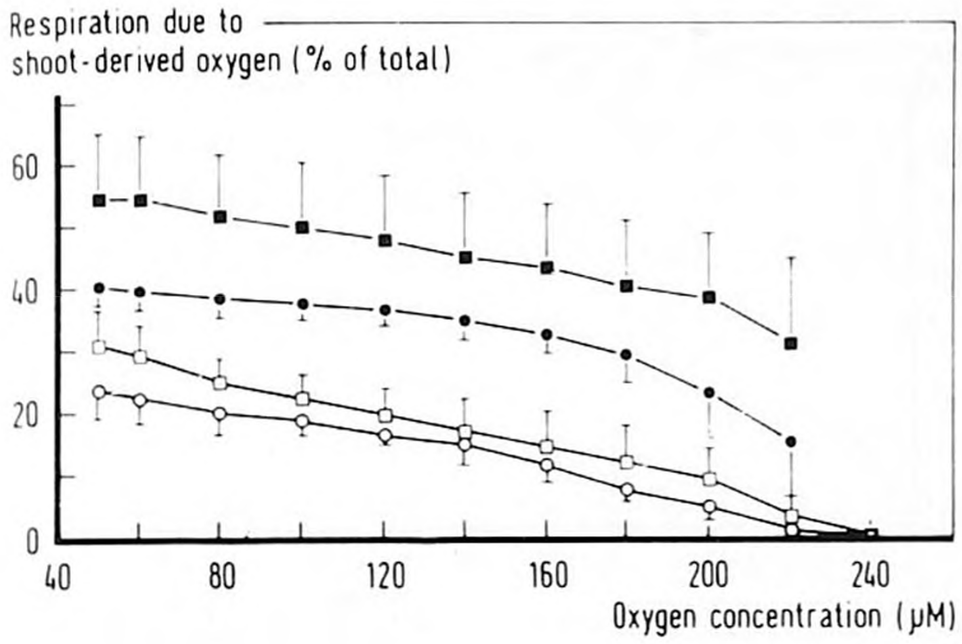

Fig. 3. Contribution of shoot-derived oxygen to root respiration (as % of total respiration) at different oxygen concentrations in the root environment of aerobically (*open symbols*) and anaerobically (*closed symbols*) grown *R. maritimus* (□, ■) and *R. crispus* (○, ●) plants (means of 2 (aerobic) or 4 (anaerobic) plants ± SE; age of the plants 5 weeks (young, aerobic plants) plus 1 — 2 weeks anaerobiosis (young, anaerobic plants))

uptake rate of plants with air in the shoot compartment decreased with decreasing oxygen concentration around the roots (Fig. 2a,c), indicating that aerial oxygen was increasingly used for root respiration. The depletion curves of young anaerobically grown plants (Fig. 2b,d), which had developed a new aerenchymatous lateral root system, showed similar patterns as those obtained from the aerobic plants. Here, internal oxygen transport could be observed in both *R. maritimus* and *R. crispus*, already at high solution oxygen concentrations, and again increasing with decreasing oxygen concentration.

Figure 3 shows the contribution of shoot-derived oxygen to root respiration in young aerobically grown plants and in anaerobically grown plants, with different amounts of newly formed, aerenchymatous roots. Two phenomena were observed for both *R. maritimus* and *R. crispus*: 1. Internal oxygen transport occurs in both aerobic and anaerobic plants and increase with decreasing oxygen concentrations in the root environment, and 2. The longer the period of anaerobiosis (and thus the more new laterals had developed), the higher the amount of internal oxygen transport (data incorporated in mean values, shown in Fig. 3). At low solution oxygen concentrations, more than 50% of the total respiration was supplied by shoot-derived oxygen in anaerobically *R. maritimus* plants, which had developed a large number of new laterals, in *R. crispus* this was at least 40% (Fig. 3, Table 1).

In *R. thyrsiflorus* internal aeration was very low, and no differences could be observed between aerobically and anaerobically grown plants (data not shown).

The responses of older plants differed from those of the young ones, in that older aerobically grown *R. maritimus* and *R. crispus* plants did not show internal oxygen transport (Table 1). With anaerobically grown old plants, internal aeration could only be observed in *R. maritimus*, and became apparent only at lower solution oxygen concentrations ($< 100\,\mu M$ O_2, data not shown). At the COPR (*ca.* $55\,\mu M$ O_2), at least 71% of the total respiration was due to shoot-derived oxygen (Table 1). In older, anaerobic *R. crispus* plants, there were no clearcut differences between the depletion curves

Table 1. Contribution of shoot-derived oxygen to root respiration at the COPR value (*ca.* $55\,\mu M$ O_2) of young and old aerobically and anaerobically grown *Rumex maritimus* and *R. crispus* plants. Data as percentages of respiration rates at $200\,\mu M$ O_2 (= 100%), being: *R. maritimus*: young aerobic 192 ± 8, old aerobic 68 ± 6, young anaerobic 192 ± 44, old anaerobic 75 ± 10, *R. crispus*: young aerobic 175 ± 54, old aerobic 70 ± 8, young anaerobic 167 ± 13, old anaerobic 56 ± 4 μmol oxygen $(g\,dry\,wt)^{-1}\,hr^{-1}$; means of 2 (aerobic plants) or 4 (anaerobic plants) replicates ± SE; age of young plants 5 weeks (aerobic plants), or 5 weeks plus 1 — 2 weeks anaerobiosis (anaerobic plants); old plants 13 weeks (aerobic plants), or 13 weeks plus 1 week anaerobiosis (anaerobic plants)

Species/age	Contribution of shoot-derived oxygen to respiration (%)	
	Aerobically grown plants	Anaerobically grown plants
R. maritimus		
young	29 ± 5	54 ± 8
old	0	71 ± 6
R. crispus		
young	22 ± 4	39 ± 2
old	0	7 ± 3

of plants with air in the shoot compartment and of decapitated plants, hence internal aeration is of minor importance (7%, Table 1).

To evaluate the ecological significance of the internal aeration process, the depletion of oxygen was measured with anaerobic *R. maritimus* plants, that were submerged to different degrees (Fig. 4). The extent of internal oxygen diffusion was determined by calculating the differences between oxygen uptake rates at the different submergence levels and of decapitated plants at the COPR-value (Fig. 5). Plants that were totally submerged showed characteristics of oxygen depletion from the root environment that were similar to those of decapitated plants. With more leaf area protruding above the water surface, the importance of internal oxygen transport increased (Fig. 5). Submergence of leaf bases and petioles resulted in a relatively sharp decrease of the apparent respiration due to internal aeration from 61 to 38% (Fig. 5), suggesting a high permeability to oxygen of these shoot parts.

Discussion

Aerial oxygen can be used for root respiration (Figs. 2, 3) and this process can contribute significantly in maintaining aerobic respiration under situations of root inundation and of partial

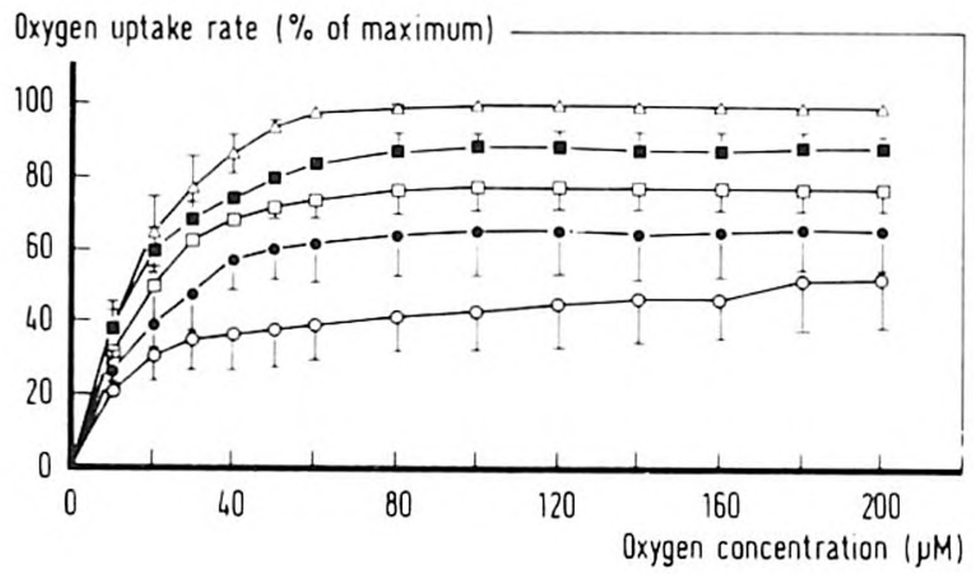

Fig. 4. Oxygen depletion profiles of anaerobically grown *R. maritimus* plants, with new lateral root system developed, at different submergence levels of the shoot (in percent of maximum oxygen uptake rate of decapitated plants at 200 μM O_2 = 100%, being 263 ± 28 μmol O_2 (g dry wt^{-1} hr^{-1}) (△ = water level 28 cm (totally submerged) and decapitated plants, ■ water level 20 cm, □ = water level 13 cm, ● = water level 7 cm, ○ = water level 0 cm (air) above shoot base (age of the plants 6 weeks plus 10 days anaerobiosis; means of 2 replicates ± SE; plants measured with shoot in the dark).

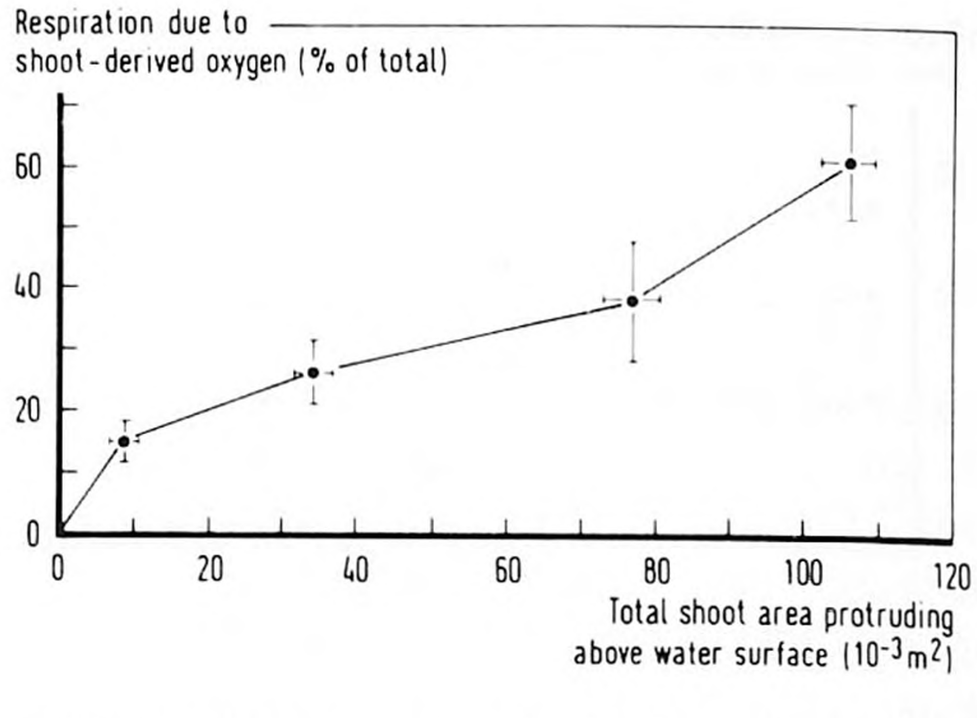

Fig. 5. Relation between root respiration due to internal oxygen transport and total area of the shoot protruding above the water surface of anaerobically grown *R. maritimus* plants at the COPR-value in the measuring system = *ca.* 50 μM oxygen; means of 2 replicates ± SE; total area of shoot material 106.1 ± 2.6 × 10^{-3} m^2).

submergence (Figs. 4, 5). The percental contribution of shoot-derived oxygen to respiration varied from at least 40% in young anaerobically grown *R. crispus* to at least 71% in old anaerobically grown *R. maritimus* plants (Fig. 3, Table 1).

The amount of internal oxygen supplied to the roots becomes more important with decreasing oxygen concentration in the root environment (Fig. 3). Although the oxygen uptake at COPR of roots of plants with air in the shoot environment is reduced compared to decapitated plants, the actual root respiration can be considered maximal and equal to the oxygen requirement of the roots of decapitated plants. Therefore, a combination of internal aeration and oxygenation from the root medium can completely satisfy the needs of the root system for oxygen, at least down to the COPR (= 50 — 60 μM). Unfortunately, the system does not allow quantification of internal aeration below the COP-value, since we do not know the actual respiration rate of the root system below COPR. However, because oxygen gradients within the plant increase with decreasing oxygen concentration in the outer solution, it is justified to state that internal aeration below COP will at least be the same and probably higher than at solution oxygen concentrations above the COP-value. Thus, internal aeration increases to 100% when oxygen is completely depleted from the root medium, regardless of the actual respiration rate.

From these results, the functional significance of the elongation of leaves and petioles of *R.*

maritimus upon total submergence, becomes apparent: by reaching the water surface, aerobic respiration can be restored through internal oxygen transport (Figs. 4, 5). Comparable results were found by Gaynard and Armstrong (1987) with *Eriophorum angustifolium* and by Atwell *et al.* (1982) with rice seedlings.

A period of anaerobiosis increased internal aeration in *R. crispus* and *R. maritimus*, when oxygen supply from the root medium is restricted (Fig. 3). The most striking response to anoxia is the formation of a new, aerenchymatous root system (Laan *et al.*, 1989a). Thus, the importance of internal aeration seems to be closely related to the formation of a new, aerenchymatous lateral root system. This was especially true for *R. maritimus*, where both young and old plants performed in this way (Table 1). Upon ageing, the leaves, tap-root and lateral roots retain a continuous porous system in this species. For *R. crispus*, however, the situation is more complicated; whilst comparable responses as in *R. maritimus* were found in young plants, older plants showed virtually no internal aeration (Table 1). In *R. crispus*, the amount of new laterals formed, their growth rate, and thus their sink activity, decreases with age, and the influence of the woody tap-root becomes increasingly important as sink for growth.

Differences in the capability of internal oxygen transport can be explained in terms of internal diffusive resistance (Armstrong, 1979; Gaynard and Armstrong, 1987), and in case of the *Rumex* species this holds for the tap-root, lateral roots and petioles. Since formation of aerenchyma reduces diffusive resistance in lateral roots (Armstrong, 1979), and aerenchyma formation takes place to the same extent in *R. maritimus* and *R. crispus* (Laan *et al.*, 1989a), the different response of the species (Table 1) must be caused by morphological differences elsewhere than in the lateral roots. Differences in tap-root porosity most likely explain the fact that old plants of *R. maritimus* are well-aerated internally, while those of *R. crispus* are not: both young and old tap-roots of *R. maritimus* have an 'open' structure, are very spongy, and as a consequence porosity is high. The tap-root of old *R. crispus* plants is much more woody and porosity is low. In young *R. crispus* plants, many new lateral roots are formed, but with age, the resistance of the woody tap-root becomes increasingly important

Table 2. Effective pore-space resistance (in $s\,cm^{-3} \times 10^5$) of 7-cm petiole segments of anaerobic *Rumex* species, illustrating the differences in continuity of gas-filled pores (means of 3 replicates ± SE)

Rumex maritimus	1.0 ± 0.3
Rumex crispus	1.5 ± 0.5
Rumex thyrsiflorus	19.7 ± 1.8

and fewer new, aerenchymatous roots develop. Although the tap-roots of young *R. crispus* plants are much less porous than those of *R. maritimus*, they are apparently open enough to enable internal gas transport (Fig. 2; Laan *et al.*, 1989b). With age, the capability of internal gas transport is lost, because the tap-root with its high diffusive resistance, is increasingly inhibiting this process. These observations fit in the idea that *R. crispus* plants, upon ageing, rely more on dormancy for survival than *R. maritimus*, which, at all ages, seems to be completely dependent on oxygen availability.

In the flood-intolerant *R. thyrsiflorus* there is no morphological basis for extensive internal gas transport: it possesses a woody tap-root with low porosity and does not form aerenchyma in the lateral root system (Laan *et al.*, 1989a). In addition, petioles of this species lack a continuity of gas-filled pores (Table 2).

The phenomenon that young aerobically grown plants of *R. maritimus* and *R. crispus* perform internal aeration equally well (Fig. 2) can be explained by assuming relatively low diffusive resistances throughout the plant, plus a high respiratory sink-activity of the lateral roots: in young plants, respiratory demand is much higher than in old plants (Table 1; Laan and Lambers, unpubl. data; Van der Werf *et al.*, 1988). Together with the fact that tap-roots are more porous, hence diffusive resistance is lower, these features together must have permitted considerable internal gas transport. On the other hand, with low diffusive resistances and a lowered sink activity, as was the case in old *R. maritimus* plants, a reverse gas transport (from root to shoot) is likely to occur when the shoot cover contains nitrogen gas. Indeed, this was recorded in old, anaerobically grown *R. maritimus* plants at solution oxygen concentrations higher than 100 μM.

In conclusion, the results show that internal longitudinal oxygen transport can be of considerable importance in maintaining aerobiosis in the

root system under hypoxic conditions; as a consequence this phenomenon can be a crucial factor in the flood-tolerance of the *Rumex* species.

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