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# NOTE

# Root-exuded oxygen in the aquatic angiosperm *Ruppia maritima**

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ABSTRACT: The potential impact of oxygen from roots on the source of inorganic nitrogen for *Ruppia maritima* L. (Potamogetonales) was investigated in laboratory experiments. Roots released oxygen at an average rate of 2 to 3 µg $O_2$ (mg dry wt)$^{-1}$ h$^{-1}$. A distinctive oxygenated zone with a radius of 0.75 to 1.25 mm developed in the sediment around the roots. Although nitrate and nitrite could have been present in the oxygenated zone, these were unlikely to be significant sources of nitrogen for *R. maritima*. Root hairs extended up to 6 mm beyond this zone. In addition, roots of plants cultured in a flow-through system took up ammonia at a rate approximately 9 times greater than that for either nitrate or nitrite.

Submerged aquatic vascular plants exhibit a variety of adaptations to their environment. In most species large air spaces are continuous throughout the plant (Sculthorpe, 1967; Bristow, 1975). Roots in anaerobic substrates rely on these air spaces for their oxygen supply from the leaves. In emergent and floating leaved plants the source of oxygen is the atmosphere (Teal and Kanwisher, 1966; Dacey, 1980). In submerged species the source of oxygen is photosynthesis (Hartman and Brown, 1967; Oremland and Taylor, 1977). As a result of this oxygen supply to the roots, oxygen can diffuse into the surrounding sediment (Wium-Andersen, 1971; Wium-Andersen and Andersen, 1972; Oremland and Taylor, 1977; Iizumi et al., 1980). This oxygen supports nitrification in anoxic sediment (Iizumi et al., 1980). The purpose of this study was to quantify oxygen release from roots of *Ruppia maritima* (Potamogetonales) and to assess the effect of this oxygen release on the source of inorganic nitrogen available to roots.

*Materials and methods.* Vegetative *Ruppia maritima* L. was obtained from flow-through cultures (Thursby, 1983). Each culture chamber had a surface area of 25 × 35 cm and a water depth of ca. 8 cm. No nutrients were added to the system, but there was a 5 cm deep substrate of beach sand. Heated seawater (22 to 24 °C) flowed into the chambers at a rate of 125 ml min$^{-1}$ resulting in a turnover rate of approximately 1 h$^{-1}$. Light was supplied by cool-white bulbs (100 to 125 µE m$^{-2}$ s$^{-1}$ at water suface, on a 16 h : 8 h, light : dark cycle). The salinity was 30 ‰.

Root apices of intact plants were isolated inside glass chambers (the upper 4 cm of screw-capped test tubes)
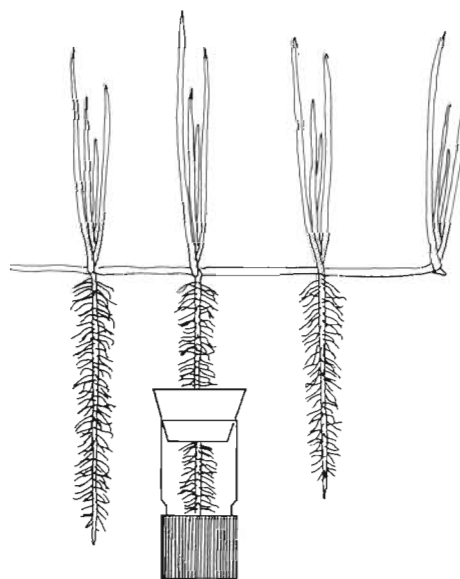


Fig. 1. Diagram of plants and oxygen chamber. Roots were threaded through a hole in a # 00 rubber stopper, and the hole sealed with anhydrous lanolin. The stopper was inserted into the bottom of a cut test tube (4 cm long), the tube filled with seawater, and capped with Parafilm and a screw-cap. The chamber was darkened with black plastic tape

darkened with black plastic tape (Fig. 1). Blank chambers (without plants) were tested as controls. Chambers were filled with 0.3 μm cartridge-filtered (Balston)* seawater, which had been bubbled with nitrogen gas to reduce oxygen content to either 10 or 50 % of air saturation. Early experiments showed that initial oxygen concentration (at least at 50 % saturation or less) in the water did not affect the release rate of oxygen.

After overnight light or dark pretreatment, plants were incubated for 1 h in a seawater bath at 30‰ salinity at 20 to 22 °C, either at an irradiance of 350 μE $m^{-2}$ $s^{-1}$ of daylight fluorescent light or in darkness. Nutrients were added to the seawater at concentrations optimal for static cultures (Thursby, 1983). At the end of the incubation period water samples were removed with a syringe, and oxygen was measured with a blood gas analyzer (Radiometer America, Inc.; Model PHM 71 Mk 2). Plants were cut at the point of insertion into the stopper, dried (80 °C) and weighed ($\pm$ 0.01 mg).

Measurements of root uptake of ammonia, nitrite and nitrate were performed in 2-compartment chambers to isolate the leaves and roots. These experiments followed procedures previously described (Thursby, 1983). Plants were used either within 1 h of removal from the flow-through system or incubated overnight with 5 μM $NaNO_3$ (for nitrate and nitrite uptake), to stimulate nitrate and nitrite reductase activity.

Width of the oxygenated zone (yellow layer) around the roots was measured on an inverted microscope with a calibrated eyepiece micrometer. To produce the oxygenated zone plants were placed into the flow-through system rooted in 150 ml of anaerobic mud in Pyrex storage dishes. After 2 wk the dishes were removed and the yellow zone measured. Roots were then washed free of sediment and the length of the root hairs recorded.

*Results.* Evidence for oxygen diffusion out of the roots of *Ruppia maritima* is shown in Table 1. Oxygen

Table 1. *Ruppia maritima.* Oxygen exudation and uptake by roots in darkened chambers (mean $\pm$ SD, n = 7)

| Overnight pretreatment | μg $O_2$ (mg dry wt)$^{-1}$ $h^{-1}$ Light | Dark |
|---|---|---|
| Light | + 1.97 $\pm$ 1.14 | + 1.04 $\pm$ 1.08 |
| Dark | + 2.93 $\pm$ 3.47* | − 0.20 $\pm$ 0.91 |

* Some plants showed a net oxygen removal

* Use of product tradename does not imply endorsement by the United States Environmental Protection Agency

diffused out of the roots when leaves were exposed to the light, and also in the dark, when plants were given a light pretreatment. Net oxygen uptake in the dark by roots was detected only if plants were pretreated overnight in the dark. Roots grown in anaerobic mud developed a distinct oxygenated layer, 0.75 to 1.25 mm thick (n = 10). The appearance of this layer was pale to bright yellow-orange, presumably due to the presence of ferric hydroxide (as suggested by Wium-Andersen and Andersen, 1972; Mendelssohn and Postek, 1982). Root hairs were abundant (ca. 60 $mm^{-1}$), their length ranging from 2.33 to 7.58 mm (n = 42) on mature roots.

Roots of plants used within 1 h of removal from the flow-through system took up ammonia approximately 9 times faster than either nitrate or nitrite (Table 2). Plants incubated overnight with 5 μM nitrate increased their rate of nitrate and nitrite uptake (20 and 90 %, respectively at 20 μM; Fig. 2), but these rates were still less than 25 % of the rate of ammonia uptake by roots.

Table 2. *Ruppia maritima.* Uptake of inorganic nitrogen by roots (mean $\pm$ S.D., n = 5). Plants were placed into uptake chambers within 1 h of their removal from the flow-through system

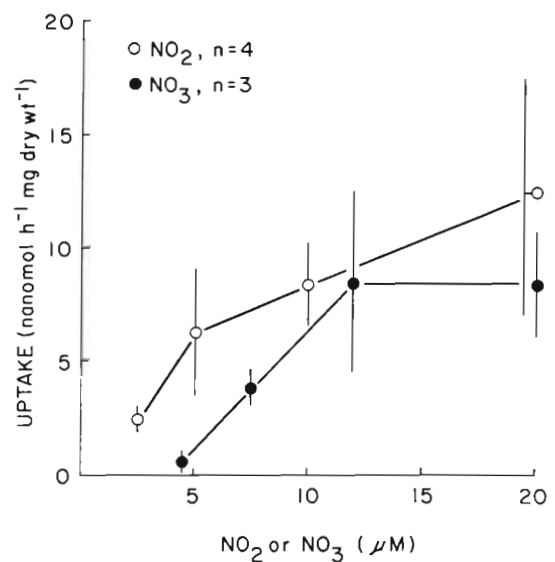| Nitrogen source | Initial conc. (μM) | Uptake rate* (nmol [mg dry wt]$^{-1}$ $h^{-1}$) |
|---|---|---|
| $NO_2$ | 20.6 | 6.9 $\pm$ 1.7 |
| $NO_3$ | 19.7 | 7.0 $\pm$ 2.5 |
| $NH_4$ | 20.5 | 60.6 $\pm$ 3.6 |

* Mean $\pm$ SD



Fig. 2. Uptake rate of nitrate and nitrite by roots of *Ruppia maritima* as a function of concentration. Prior to experiment, plants were supplied overnight with 5 μM of $NaNO_3$. Each point represents the mean $\pm$ SD

*Discussion.* The lacunal system of *Ruppia maritima* can function as an oxygen reservoir. Roots showed a net removal of oxygen from the water in darkness only when pretreated in the dark. Some roots continued to show a net oxygen release in the dark if the plants were given a light pretreatment. Lacunae of *Elodea canadensis* and *Ceratophyllum demesum* also store oxygen (Hartman and Brown, 1967). Oxygen release rates for roots of *R. maritima* were generally less than those reported for freshwater aquatic vascular plants (Armstrong, 1964; 1967), but greater than that for the seagrass *Zostera marina* (Iizumi et al., 1980).

Nitrification can take place in the rhizosphere, if oxygen is present. Roots of *Ruppia maritima* plants from the flow-through culture system, however, clearly show greater ammonia uptake than that for either nitrate or nitrite. Ammonia concentrations in interstitial water of marine sediments can exceed 100 μM (Hopkinson and Wetzel, 1982; Kenworthy et al., 1982; Iizumi et al., 1982). This is sufficient to saturate ammonia uptake by roots in *R. maritima* (Thursby, 1983). In addition, in the presence of ammonia root uptake of nitrate is negligible (Thursby, 1983). Root hairs of *R. maritima* extended beyond the narrow aerated zone immediately surrounding the roots by as much as 6 mm. Any nitrate or nitrite in the anaerobic sediment would be restricted to the aerated zone. Since root hairs constitute the primary absorptive site in roots (Salisbury and Ross, 1978), the roots may not have ready access to any available nitrate or nitrite.

Oxygen release by roots is more than a result of the necessity of supplying oxygen to the roots. An oxidized layer around the roots of plants in anaerobic substrates can reduce the potential for manganese or iron toxicity, as well as render ethylene, $H_2S$ and certain organic acid harmless (Foy et al., 1978; Mendelssohn, 1979). This may serve as the primary function of the oxygenated layer around the roots of *Ruppia maritima*.

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