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Preservation of nitrifying capacity and nitrate availability in waterlogged soils by radial oxygen loss from roots of wetland plants

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Abstract The effects of radial O_2 loss from roots on nitrification and NO_3^- availability were studied. Plants of the flooding-resistant species *Rumex palustris* and the flooding-sensitive species *Rumex thyrsiflorus* were grown on drained and waterlogged soils with an initially high nitrifying capacity. Nitrate reductase activity in the plant leaves was used as an indicator of NO_3^- availability to the plants. In a separate experiment these species were shown to have higher levels of nitrate reductase activity when NO_3^- was added to the soils compared to when only NH_4^+ was provided. In drained soils nitrification was maintained and both plant species showed relatively high nitrate reductase activities in their leaves. In the waterlogged series planted with *R. thyrsiflorus*, nitrification was inhibited, NH_4^+ accumulated, and the plants grew less well compared to those on drained soils. In contrast, waterlogged soils planted with *R. palustris* had a redox potential high enough for O_2 to be continuously replenished. Furthermore, the nitrifying capacity of these latter soils was maintained at a high level. *R. palustris* grew well and NO_3^- must have been available to the plant, since a high level of nitrate reductase activity was observed in the leaves.

Key words Radial O_2 loss · Nitrification · Waterlogging · *Rumex thyrsiflorus* · *Rumex palustris* · Nitrate reductase · Redox potential

Introduction

Many plants, especially calcicole species, prefer to take up N either as NO_3^- or as a combination of NO_3^- and NH_4^+ (Bogner 1968; Ellenberg 1977; Gigon and Rorison 1972). In natural soils, nitrification is probably the most important source of NO_3^-. This oxidation of NH_4^+ via NO_2^- to NO_3^- is generally performed in two separate steps by chemolithotrophic nitrifying bacteria (Watson et al. 1989). The process of nitrification depends strongly on the O_2 status of the environment because of the O_2 dependency of the NH_4^+-oxidizing enzyme, ammonium mono-oxygenase (Belser 1979). Upon waterlogging, the rate of diffusion of O_2 into the soil decreases sharply (Armstrong 1979), whereas the O_2 demand by the soil is maintained by the activity of plant roots and soil organisms. Hence anoxic conditions will occur (Ponnamperuma 1984). At this point nitrification will no longer take place and NH_4^+ accumulates (Laanbroek 1990).

The ability of certain plants to survive in these anoxic soils is generally increased by the presence of aerenchyma in their roots (Justin and Armstrong 1987; Laan et al. 1989a). Radial O_2 loss from aerenchymatous roots to the rhizosphere creates a small sheet of oxidized substrate around the root in an otherwise reduced environment (Laan et al. 1989b). Possibly, in this sheet the nitrifying population is still active, providing the plant with NO_3^-. Both et al. (1992) found a larger nitrifying population in the oxidized rhizosphere of *Glyceria maxima* compared to the reduced bulk soil. However, in a previous experiment we observed no stimulation of nitrification by the flooding-resistant *Rumex palustris* species, which contains aerenchyma in its roots, under waterlogged conditions (Engelaar et al. 1991). We found that NH_4^+ and not O_2 was probably limiting the activity of the nitrifying bacteria in the rhizosphere of this *Rumex* sp.

The aim of the present study was to investigate whether the nitrifying capacity of a waterlogged soil can be maintained by the presence of a plant species with aerenchymatous roots, provided that NH_4^+ is not a limiting factor. The experiment was performed with *R. palustris*, a flooding-resistant and O_2-releasing species that forms aerenchymatous laterals under waterlogged conditions (Laan et al. 1989a; Voesenek et al. 1989), and *R. thyr-*

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siflorus a flooding-sensitive, non-O_2-releasing species (Laan et al. 1989; Blom et al. 1990).

Materials and methods

Two experiments were performed. In the first experiment the use of nitrate reductase activities as a measure of NO_3^- availability, as suggested previously (Uhel et al. 1989; Langelaan and Troelstra 1992), was validated for the two species studied. In the second experiment the positive effect of a flooding-resistant plant species on nitrification capacity and NO_3^- availability in a flooded soil was investigated.

Seeds of *R. palustris* and *R. thyrsiflorus* were collected from floodplains in the Rhine delta, near Nijmegen, The Netherlands. After removal of the perianth, the seeds germinated on moist filter paper in Petri dishes, at a temperature of 10 °/27 °C with a 12 h night/12 h day.

Nitrate reductase activity as a measure of NO_3^- availability

Sixty-three light-proof plastic pots were prepared for each species. They were filled with 500 g air-dried, sieved (mesh size 2 mm), calcareous river sand [pH(H_2O) 7.7] low in organic matter, collected from floodplains in the Rhine delta (Bemmel, The Netherlands). Each pot was supplied with 0.86 mmol KH_2PO_4, 0.63 mmol K_2SO_4, 0.36 mmol $MgSO_4 \cdot 7\,H_2O$, 10 µmol Fe-ethylenediamine-di(o-hydroxyphenyl acetic acid) and 4.2 mmol N. The N was added as $NaNO_3$, NH_4NO_3 or $(NH_4)_2SO_4$, each form to 21 pots. In the case of $(NH_4)_2SO_4$ half the N was applied at the start and the other half after 2 weeks. To all pots 5 mg dicyandiamide, a nitrification inhibitor (Amberger 1986), was added. Analyses of soil mineral N at the end of a control experiment without plants showed that the dicyandiamide maintained its inhibitor action throughout the entire experimental period. The sand in the pots was brought to 60% water-holding capacity by adding 156 ml demineralized water. One seedling of either *R. palustris* or *R. thyrsiflorus* was planted in each pot and the pots were placed in growth chambers with a day period of 16 h, a photosynthetic photon flux density of 200±20 µE $s^{-1}\,m^{-2}$, and a temperature of 25 °C. At night, the temperature dropped to 15 °C. Relative humidity was kept constant at 55–70%.

After 5 weeks, the nitrate reductase activity was determined 1, 5, 10, and 14.5 h after the start of the light period and 0.5, 4, and 7 h after the start of the dark period. At each sampling time three plants per species were sampled, and the analyses were carried out in triplicate for each plant, on the youngest two or three fully developed leaves. The method used was a modification of the assay described by Jaworski (1971). The leaves were separated from the shoot, combined for each plant, and cut into segments of 0.5×0,5 cm after removal of the nerve. Between 100 and 200 mg of these segments was placed in 25-ml flasks wrapped in aluminium foil, containing 4 ml 0,25 *M* phosphate buffer (pH 7.8) with chloramphenicol (0.5 mg/ml). After two 1-min periods of vacuum infiltration, 1 ml 0.2 *M* KNO_3 solution containing 1-propanol (75 µl/ml) was added, and the flasks were sealed with a rubber stopper. Samples of 0.4 ml were taken after 30 and 60 min of incubation at 30 °C in a shaker (60 rpm). The NO_2^- accumulation was measured colorimetrically using a photospectrometer (Vitatron). Since the incubation was performed in the dark, NO_2^- reduction to NH_4^+ was inhibited (Beevers and Hageman 1969).

Nitrification and NO_3^- availability in waterlogged soils

Experimental design

A series of 50 glass beakers (600 ml) were filled with 704 g moistened soil. This soil consisted of five parts (dry weight) Bemmel sand and one part (dry weight) of the upper 5 cm of an extensively used, calcareous, sandy, grassland soil [pH(H_2O) 7.6], both sieved (mesh size 2 mm). The grassland soil had been collected from floodplains of the Yssel (Brummen, The Netherlands). The Brummen soil was used as an inoculum of nitrifying bacteria and had been collected within 2 weeks of the start of the experiment. The pots contained 104 g water, bringing the dry soil to 60% water-holding capacity. All pots were wrapped with aluminium foil to make them light-proof. One seedling of either *R. palustris* or *R. thyrsiflorus*, with two fully developed leaves, was planted in each of the 50 pots. Nutrition was added to the pots as a modified Hoagland solution (Hoagland and Arnon 1950), NO_3^- being replaced by NH_4^+ in combination with SO_4^{2-}. This solution was added in exponentially increasing quantities, once a week, until week 7. From that time onwards the maximum weekly dose was applied, comprising (per pot) 2.24 mmol NH_4^+, 0.28 mmol $H_2PO_4^-$, 0.84 mmol K^+, 0.14 mmol Mg^{2+}, and 1.12 mmol SO_4^{2-}. The solution was injected at the bottom of the pot. From week 4 onwards additional NH_4^+ was supplied once a week, at 1, 1.5, and 2 mmol per pot in weeks 4+5, 6+7, and 8+9, respectively. The soils were kept at a constant moisture content by daily watering with demineralized water.

By week 4, the plants had become large enough for the first sampling. Five plants of each species were sampled. Half the remaining pots were waterlogged at this time, taking care that the shoots stayed out of water. Another five drained and five waterlogged pots were sampled for each species in weeks 6 and 10. The youngest fully developed leaves were removed from the plants and used for analyses of nitrate reductase activity. Afterwards, the shoots, roots, soil, and, for the waterlogged pots, the water phase were separated. The shoots and roots were washed with tap water.

Chemical analyses

We analyzed several parameters as indicators of the three basic components of nitrification, O_2, NH_4^+, and an active nitrifying population. Any NO_3^- produced was checked by measuring the NO_3^- content of the soil and by using the nitrate reductase activity of the leaves as an indicator of NO_3^- uptake by the plants.

To measure the redox potential, four pots of each plant species, two waterlogged and two drained, were provided with a platinum electrode in week 4. The electrode consisted of a PVC shaft with a platinum rod at the end (10 mm long, 1.5 mm in diameter) and was placed at the side of the pot 2–5 cm above the bottom. From this time onwards the redox potentials of the soils were measured regularly with this platinum electrode, a reference electrode ($Hg/HgCl_2$/saturated KCl, Metrohm, type 60701.100), and a mV meter (Metrohm, type E488).

To measure the dry weight of plants and soils, the roots, shoots, and 10 g of moist, homogenized soil per pot were dried separately for 24 h at 70 °C.

Soil extracts for mineral N measurements were prepared by shaking 50 ml 1 *M* KCl solution and 10 g moist soil (100 rpm) for 2 h at 20 °C. After centrifugation (5 min, 10000 rpm), NH_4^+ and NO_3^- concentrations were determined in the supernatant using a Technicon Traacs 800 autoanalyzer. The mineral N concentration in the water phase of the waterlogged pots was also determined after centrifugation, and added to the mineral N content of the corresponding soils.

To measure the nitrifying capacity of the soil, accumulations of NO_2^- and NO_3^- were measured in 250-ml flasks, containing 40 g moist soil, 0.2 g $CaCO_3$, and 100 ml medium, over a 6-h period. The medium contained 2.5 m*M* $(NH_4)_2SO_4$ and 1 m*M* P buffer (pH 7.5) shaken at 150 rpm and 25 °C. One-milliliter samples were taken from the flasks after 0.5 and 6 h of incubation and NO_2^- and NO_3^- concentrations were measured as described above. Preliminary experiments had demonstrated a linear production of NO_3^- and NO_2^- during this 5.5-h period. The assay for nitrate reductase activity was the same as in the first experiment. As a result of that experiment, samples were taken 4 h after the start of the light peri-

od. Depending on the available biomass, one to three replicates were measured per plant.

Statistical analysis

Differences between treatments and sample times within one plant species were analyzed by means of the Wilcoxon two-sample test (Sokal and Rohlf 1981).

Results

Nitrate reductase activity as a measure of NO_3^- availability

R. palustris showed a significantly higher nitrate reductase activity at all times of day when N was supplied as either NO_3^- or a combination of NH_4^+ and NO_3^- than when only NH_4^+ was added (Fig. 1). The same effect was observed in *R. thyrsiflorus* from 1 h before to 10 h after the start of the light period. On the basis of these results, the sampling time for the waterlogging experiment was set at 4 h after the start of the light period, with basic values (NH_4^+ addition only) of approximately 2 µmol NO_3^- per g dry weight per hour for both species.

Nitrification and nitrate availability in waterlogged soils

The redox potentials measured in the soils are shown in Fig. 2. Differences between duplicate measurements in any one series ranged from 5 to 50 mV. Both well drained series remained at a constant value of approximately 450 mV throughout the experiment. Upon waterlogging, the soils with either species showed an initial reduction of the redox potential. Soils with *R. thyrsiflorus* reached a constant value of 250 mV after 28 days, but soils with *R. palustris* remained constant at a higher potential, 350–390 mV, from day 25 onwards.

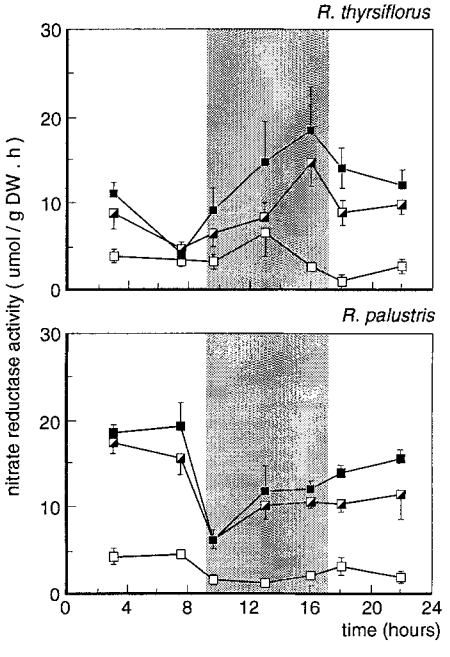

Fig. 1 Mean leaf nitrate reductase activities (±SD, $n = 3$) of *Rumex thyrsiflorus* and *R. palustris* plants supplied with either $NaNO_3$ (■), NH_4NO_3 (◪), or $(NH_4)_2SO_4$ (□) throughout a 24-h period. The *grey area* represents the dark period. *DW* dry weight

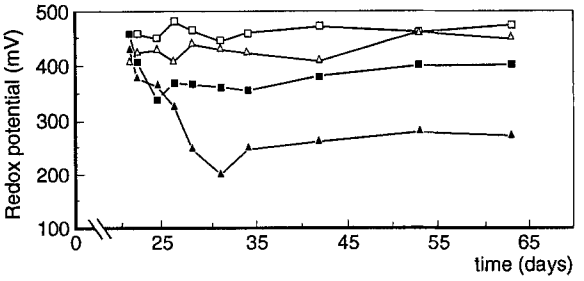

Fig. 2 Redox potentials in well drained (*open symbols*) and waterlogged (*closed symbols*) soils planted with either *Rumex thyrsiflorus* (*triangles*) or *R. palustris* (*squares*). Waterlogging started on day 21. Means of two replicates are shown

All plants survived, except for one *R. thyrsiflorus* of the waterlogged series. The waterlogged *R. thyrsiflorus* plants produced significantly less shoot biomass by week 6 and less root and shoot biomass after week 10 compared to the plants with better drainage (Fig. 3). In week 6, the waterlogged *R. palustris* plants also had less biomass compared to the plants with better drainage but by week 10 the waterlogged plants had produced the largest biomass.

As shown in Table 1, N was available in every soil, either as NH_4^+ or NO_3^-, throughout the experiment. In all well drained soils NO_3^- was the predominant N form. Upon waterlogging NH_4^+ became the most important N form in the soil for both plant species. In contrast to waterlogged soils planted with *R. thyrsiflorus*, NO_3^- was still present in week 6 in the waterlogged soils planted with *R. palustris* and far less NH_4^+ accumulated in these soils towards the end of the experiment. The nitrifying capacity of the well drained soils increased from week 4 to week 6 and then remained fairly constant (Fig. 4). The major difference between the two species occurred in the waterlogged soils. With *R. palustris* these soils showed an increase in nitrifying capacity from weeks 4 to 6, followed by a small decrease from weeks 6 to 10, resulting in a return to the nitrifying capacity of week 4. In contrast, the waterlogged soils planted with *R. thyrsiflorus*, maintained a constant nitrifying capacity from weeks 4 to 6 followed by a major decrease, so that in week 10 the nitrifying capacity was approximately 10% of that in week 4.

The nitrate reductase activity (Fig. 5) in the leaves seemed to be a good reflection of the $NH_4^+ : NO_3^-$ ratio in the soil, as presented in Table 1. In all pots where NO_3^- was an important part of the soil mineral N nitrate reductase activity was relatively high. The only exceptions were the *R. palustris* plants in waterlogged soils after 10

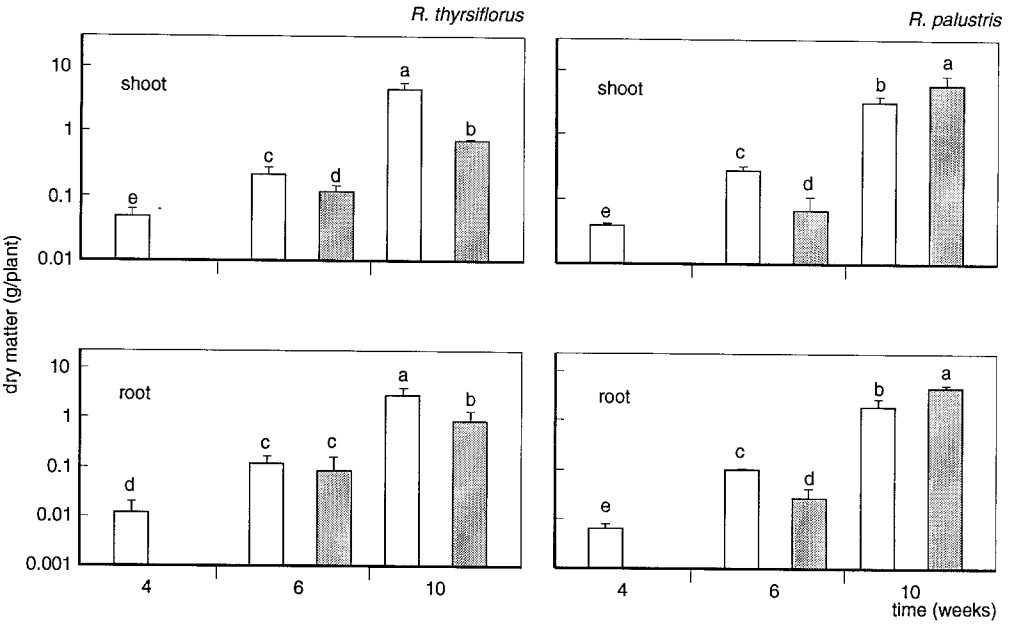

Fig. 3 Mean dry-matter accumulation of shoots and roots of *Rumex thyrsiflorus* and *R. palustris* in well drained soils (*open bars*) and waterlogged soils (*grey bars*). Values are ±SD, $n = 4-5$. In week 4 the *bars* indicating the drained soils also represent the starting point of the waterlogged series. Different *letters* above the bars indicate significant differences between soils or sampling times ($P \leq 0.05$)

weeks, which combined high nitrate reductase activity with a high $NH_4^+ : NO_3^-$ ratio.

Discussion

The first experiment showed that the nitrate reductase activity of leaves of both plant species was a good indication of NO_3^- availability in the soil throughout a large part of the day and night. This affirms the higher nitrate reductase activity in leaves of plants supplied with NO_3^- compared to plants supplied only with NH_4^+, as reported before (Barro et al. 1991; Langelaan and Troelstra 1992).

It is very likely that nitrification took place in the waterlogged soils with *R. palustris*. According to other studies the measured redox potential was high enough to expect the presence of O_2 (Pearsall and Mortimer 1939; Turner and Patrick 1968; Watanabe and Furusaka 1980), which is needed for the nitrification process. Also, the nitrifying capacity remained at a high level after waterlogging. The relatively low mineral N content of the waterlogged soils planted with *R. palustris* (Table 1) can be explained by the large N accumulation in the biomass (Fig. 3). Although no precise N balance could be calculated, an estimate of the N retrieved was made. On the basis of previous experiments, the N content of the plants was assumed to be 1500 µmol per g dry weight. The estimates of N incorporated in the plant biomass plus mineral N in the soil were 14.4 and 15.0 mmol for the well drained and waterlogged pots, respectively, planted with *R. thyrsiflorus* and 18.1 and 16.4 mmol for those planted with *R. palustris*. For *R. thyrsiflorus*, this accounted for 72 and 75% of the total of 20 mmol N applied to each pot in well drained and waterlogged soils, respectively. For *R. palustris*, this accounted for 91% in the well drained pots and 82% in the waterlogged pots. Since N recoveries in the waterlogged and well drained pots were high and almost equal, N losses as a result of NO_3^- reduction or immobilization could not have been very high, in contrast to

Table 1 Mean NH_4^+ and NO_3^- concentrations (µmol g^{-1} dry weight) in drained (*D*) and waterlogged (*W*) soils, with either *Rumex thyrsiflorus* or *R. palustris* (±1SD, $n = 4-5$). Waterlogging started in week 4. The values of the drained soils in week 4 also represent the starting point of the waterlogged series. Different *letters* indicate significant differences between soil or sampling times within one species ($P \leq 0.05$)

Week number	Soil type	NH_4^+	NO_3^-	Ratio $NH_4^+ : NO_3^-$
R. thyrsiflorus				
4	D	0.11 ± 0.03a	1.17 ± 0.29b	0.09 ± 0.01d
6	D	1.38 ± 0.60b	5.49 ± 1.38a	0.25 ± 0.07c
	W	3.94 ± 0.92c	0.29 ± 0.25c	144 ± 277b
10	D	2.30 ± 2.47bc	5.41 ± 8.59ab	0.57 ± 1.03cd
	W	21.02 ± 4.46d	0.004 ± 0.004d	4832 ± 2556a
R. palustris				
4	D	0.06 ± 0.00d	5.13 ± 0.91c	0.01 ± 0.00d
6	D	0.33 ± 0.37c	11.8 ± 2.13b	0.05 ± 0.04c
	W	6.06 ± 0.73a	3.79 ± 0.11d	1.68 ± 0.19b
10	D	1.72 ± 2.38bc	16.7 ± 4.76a	0.11 ± 0.14c
	W	3.96 ± 3.53bc	0.06 ± 0.05e	46.7 ± 40.5a

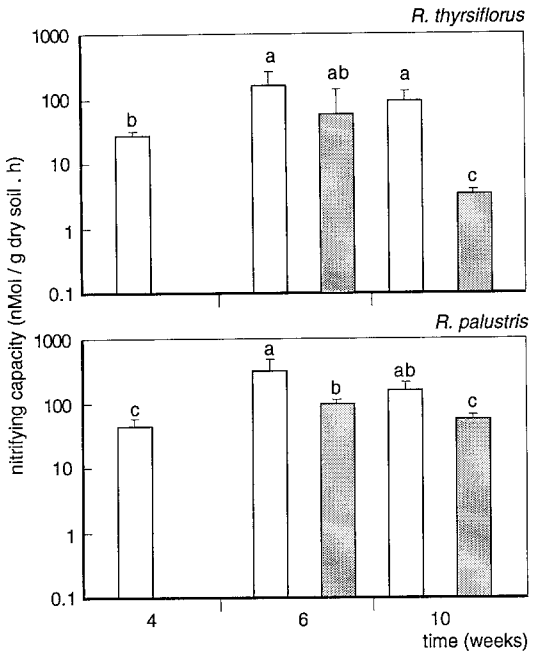

Fig. 4 Mean nitrifying capacity of drained soils (*open bars*) and waterlogged soils (*grey bars*) planted with either *Rumex thyrsiflorus* or *R. palustris*. For other explanations see Fig. 3

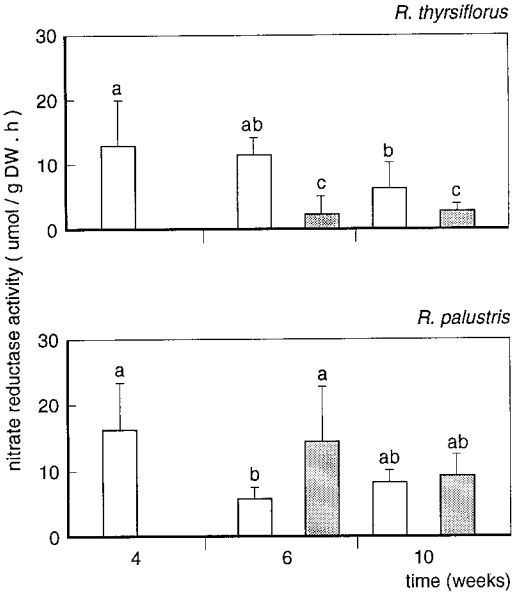

Fig. 5 Mean nitrate reductase activity in leaves of *Rumex thyrsiflorus* and *R. palustris* grown on drained soils (*open bars*) and waterlogged soils (*grey bars*). *DW* dry weight; for other explanations see Fig. 3

a previous experiment (Engelaar et al. 1991). The high nitrate reductase activity of *R. Palustris* grown in waterlogged soils (Fig. 5) indicates that at least a part of this N was taken up as NO_3^- (Langelaan and Troelstra 1992). The nitrate reductase activity in both the waterlogged and the well drained *R. palustris* plants was higher than the basal level found for NH_4^+ nutrition (Figs. 1, 5). The exception of the high nitrate reduction activity in combination with a high $NH_4^+ : NO_3^-$ ratio observed for the waterlogged soils planted with *R. palustris* can then be explained by a high rate of NO_3^- uptake by the plant, possibly in combination with some NO_3^- reduction in anoxic sites in the soil.

No nitrification took place in the waterlogged soil planted with *R. thyrsiflorus*. The applied NH_4^+ accumulated in the soil (Table 1) and the nitrifying capacity decreased drastically (Fig. 4). The relatively low nitrate reductase activity of plants grown on waterlogged soil, approximately basal level, indicated that N had predominantly been taken up as NH_4^+ by the plant (Figs. 1, 5). In contrast, nitrification did occur in the well drained soil where the nitrifying capacity increased during the experiment (Fig. 4) and NO_3^- was produced. In these pots the nitrate reductase activity was significantly higher, indicating that NO_3^- was available to the plants. Thus inhibition of nitrification in the presence of *R. thyrsiflorus* was a direct result of the waterlogging treatment, which resulted in anoxia, as illustrated by the low redox potential (Fig. 2). The redox potential was below the critical value for the presence of O_2 (Turner and Patrick 1968). It remained constant at 250 mV, a value at which NO_3^- usually becomes reduced (Patrick 1960). The stabilization at this redox level might have been the result of a poising effect by NO_3^- that was already present at the start of waterlogging (Gambrell and Patrick 1978) or by a slow downward diffusion of small amounts of NO_3^- from the better oxygenated water layer.

In contrast to our previous experiment (Engelaar et al. 1991) no negative correlations were found between the plant biomass and the nitrifying capacity of the soil, excluding the possibility that soluble root exudates may have affected nitrification. In fact, in the waterlogged pots of *R. palustris* in week 10, nitrifying capacity was positively correlated shoot biomass ($P \leq 0.01$). This might have been the result of a larger radial O_2 loss, and subsequent stimulation of the nitrifying capacity, by a larger plant. Still, there seemed to be a tendency for the nitrifying capacity to show a slight decrease, even in those treatments where sufficient O_2 and NH_4^+ were available, in the well drained series of both species and the waterlogged series of *R. palustris*. This effect was also evident in previous experiments (unpublished data) and cannot yet be explained. It is highly unlikely to be the result of an NH_4^+ limitation since no negative correlation with the plant biomass nor any positive correlation with the NH_4^+ content of the soil was found. Compared to the effects of waterlogging on *R. thyrsiflorus*, inhibition of nitrification in the presence of *R. palustris* was only of minor importance.

We therefore conclude that waterlogging in the presence of *R. thyrsiflorus* resulted in anoxia, a depressed nitrification capacity, and an accumulation of NH_4^+ in the soil. When the soil remained aerated through radial O_2 loss, as happened with *R. palustris*, the redox potential and nitrifying capacity of the soil remained at a far

higher level. Since the possibility of an NH_4^+ limitation can be excluded, the three basic conditions needed for nitrification, O_2, NH_4^+, and a potentially active nitrifying population, were all present in these soils. That nitrification actually took place in waterlogged soils planted with *R. palustris* was demonstrated by the high nitrate reductase activities in the leaves of these plants, which indicated uptake of NO_3^-.

These results, together with those reported previously (Engelaar et al. 1991), indicate that nitrification can be maintained in the rhizosphere of a plant with aerenchymatous roots under waterlogged conditions, but only when sufficient NH_4^+ is present to support both the plant and the total microbial population.

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