

## Root growth of *Rumex* and *Plantago* species in compacted and waterlogged soils

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### SUMMARY

The root patterns of *Rumex palustris* (Sm.), *Rumex acetosa* (L.) and *Plantago major* (L.) ssp. *major*, three species occurring in the river forelands, were studied in experimentally waterlogged or drained compacted soils and compared with specimens growing in drained loosely packed-soils as a control. A modified method for endoscopy in root boxes was developed. The species studied showed different patterns of root development as a result of soil waterlogging or compaction. *R. palustris* was the least sensitive to waterlogged soils, as shown by the formation of new, morphologically distinctive roots; *R. acetosa* was the most sensitive and *P. major* had an intermediate response. With respect to soil compaction *P. major* was the least affected species, followed by *R. acetosa* and *R. palustris*, respectively. The fractional root porosity of these species was studied by using a flow-through system to create hypoxia, a small soil-pore diameter or a combination of both. Hypoxia resulted in a higher root porosity. In both *Rumex* species small soil-pores inhibited this increase. Contrasting results were found for the porosity of *Plantago* roots. Results are discussed in relation to the distribution of these species in the field.

*Key-words:* aerenchyma formation, perforated soil system, relative extension rates, spatial distribution of roots.

### INTRODUCTION

Roots of plants occurring in river forelands have to cope with extreme changes in soil conditions. Two of the most obvious features of those areas are fluctuating water tables and soil compaction. As a result of high water levels the rhizosphere may become hypoxic or even anoxic during flooding (Ponnamperuma 1984; Gambrell *et al.* 1990) and oxygen, which is necessary for respiration, may no longer be available to the roots from its surroundings. In the times between flooding soil compaction may occur. The process of intermittent water application makes the soil more dense by breaking down large soil particles during periods of water saturation (Hadas 1990). The resultant particles are then strongly bound by contraction of the hydration envelope of the colloidal units as the soil water content decreases (Samani & Yitayew 1989; Hadas 1990). A second cause of soil compaction is trampling. Cattle paths can often be found parallel to the levees and dikes and fences, or along the river bank, and are more or less frequently flooded depending on their location in the flood plains. Soil compaction may lead to increased mechanical resistance as well as reduced gas diffusion (Boone *et al.* 1986).

The formation of a high fractional root porosity, for instance as aerenchyma, has proved to be essential to meet the oxygen demands of roots in hypoxic or anaerobic conditions (Laan *et al.* 1990) and is considered to be a good indication of the flood resistance of a species (Justin & Armstrong 1987; Laan *et al.* 1989). However, in compacted soil the root may face hypoxia and increased mechanical impedance at the same time. Aerenchyma formation can overcome the effects of hypoxia in these soils but it may also weaken the root structure. Root growth depends both on the ability of the root tips to evade or overcome mechanical pressures (Taylor 1974) and on their oxygen supply via the soil or internal aeration (Tackett & Pearson 1964; Webb & Armstrong 1983). Therefore, root patterns of plants in the river forelands should be expected to change swiftly with the physical conditions of the soil before, during and directly after waterlogging.

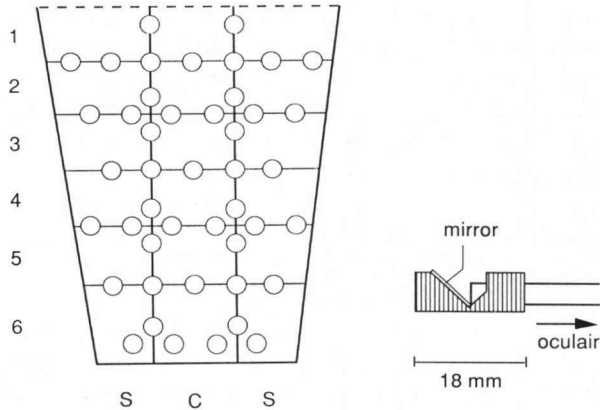
There is a gap in our knowledge with respect to plant root patterns in waterlogged or compacted soils, primarily because of a lack of suitable methods for studying intact root systems (Böhm 1979; Harper *et al.* 1991). Many of the methods described in the literature are essentially destructive, being based on excavation of the root system or at least part of it. Others, e.g. observations with glass tubes (Bates 1937; Waddington 1971; Böhm 1974) and rhizotrons (Taylor *et al.* 1990) are non-destructive but large tubes cannot easily be used in well-defined pot experiments and smaller tubes sample only a small volume of soil making it difficult to obtain a clear picture of the complete root architecture (Mackie-Dawson & Atkinson 1991). In rhizotrons the roots cannot grow undisturbed but are forced downwards or sideways after reaching the glass wall. A suitable, non-destructive method is essential when root growth rates of individual plants are to be calculated. The introduction of the perforated soil system (Van den Tweel & Schalk 1981; Bosch 1984) made it possible to study the root development and architecture of individual plants accurately over a period of time. It was even possible to derive relative root-growth rates (Voeselek & Blom 1987). However, because of the perforations bored through the soil monolith, it was not possible to study root growth and distribution in waterlogged or compacted soils. We designed a combination of the perforated soil system and the mini-rhizotron technique to study root growth and spatial distribution accurately in both situations.

This paper aims to test the hypothesis that flooding and soil compaction, at least partially, determine the root anatomy and thus the root patterns of three *Rumex* and *Plantago* species. The relationship between these root characteristics and the distribution of these species in the river area will be discussed. The investigated species are: *R. acetosa* from high, seldom flooded habitats; *R. palustris*, from low lying, frequently flooded habitats (Blom 1990; Blom *et al.* 1990); and *P. major* ssp. *major*, on and along heavily trampled cattle paths (Blom 1976; Kutschera 1960).

## MATERIALS AND METHODS

### *Root patterns*

*Experimental design.* Three series of 24 root boxes with either *Rumex palustris* (March 1990), *Rumex acetosa* (November 1990) or *Plantago major* ssp. *major* (March 1991) were prepared. Per series eight had drained, loosely packed substrates (control series), eight had drained, densely packed soils and eight were waterlogged during the course of the experiment. A modification of the horizontally perforated soil system (Voeselek & Blom 1987)



**Fig. 1.** Modifications of the perforated soil system (Voeselek & Blom 1987) for root observations in waterlogged or compacted soils. Root box with positions of the glass tubes dividing the soil in six horizontal layers and three vertical columns (two side columns and one centre column). Detail of the intrascope top with dismountable mirror is presented separately.

was used. Forty-five perforations were placed in our experiment, resulting in six horizontal layers and three vertical columns (Fig. 1). A mirror was placed at an angle of 45° on top of the intrascope (Fig. 1). Four boxes were perforated for each treatment and provided with glass tubes (diameter 12 mm), which prevented collapse of the soil and root damage during counting. The other four were unperforated and served as blanks in order to test the possible effects of the glass tubes on plant development.

**Preparations.** The root boxes were filled with an air-dried, sieved (2-mm mesh size) river sand:clay mixture (1:3, v:v). In the drained, loosely packed series, the mixture was moistened to 60% of its water holding capacity and the bulk density of these soils was 1.41 g cm<sup>-3</sup>. Compaction (bulk density = 1.49 g cm<sup>-3</sup>) was achieved by percolating water over the soil after sealing the boxes water tight, except for some perforations. The boxes in the waterlogged series were fitted with a plastic bag on the inside and, after sealing them water tight, filled with water-saturated soil mixture (bulk density = 1.47 g cm<sup>-3</sup>). All boxes were prepared at least 72 h before planting the seedlings, thus excess water could evaporate.

Seeds of the different species were collected in forelands of the Waal River near Nijmegen (The Netherlands). They were germinated on moistened filter paper in petri dishes after removal of the perianth. During the 8 h dark/16 h light period temperatures were 10°C/25°C for both *Rumex* species and 10°C/27°C for *P. major* ssp. *major*, respectively. Plants were placed in the root boxes, one per box, when they had two fully developed leaves. The root boxes were placed in a greenhouse under a minimum photoperiod of 16 h created by sodium (SON-T 400 W, Philips) and mercury lamps (HLRG, Philips) at a light intensity of 120 μEinstein s<sup>-1</sup> m<sup>-2</sup>; the temperature was 19°C during the night and 20–24°C during the day. The topsoil and the sides of the drained boxes were regularly sprayed with tap water.

**Measured parameters.** As soon as at least one root was detected in any one box the number of roots per glass tube was counted at regular intervals, i.e. 7 days for *R. palustris* and *P. major* ssp. *major* and 3 days for the faster extending *R. acetosa*. When the roots in the control boxes had reached the second horizontal row of glass tubes, the designated

boxes were waterlogged by placing them in large containers with tap water ( $14^{\circ}\text{C} < T < 20^{\circ}\text{C}$ ) with the water level 1 cm above the soil surface. The leaves were in contact with the atmosphere at all times. The experiment was terminated when the roots in one of the boxes reached the bottom or the side of the box. Shoot dry weight ( $70^{\circ}\text{C}$ , 48 h) was then measured. After a final count of the roots, the soil monolith was cut into six horizontal layers and three vertical columns (Fig. 1, a total of 18 segments). The roots were washed out per segment and both of the side segments per layer were combined. Root lengths were measured per segment by means of the line intersect method (Newman 1966) using a Comair root length scanner (Comair, Melbourne, accuracy 0.1 m). The dry weight of the root system was also determined ( $70^{\circ}\text{C}$ , 48 h).

At the end of the experiment the mechanical resistance of the soils was measured 18 h after the daily watering by means of a penetrometer with a conus of  $2\text{ cm}^2$  (tip angle =  $60^{\circ}$ ). The resistance differed significantly between the three treatments being 0.38 (SD = 0.02), 0.60 (SD = 0.05) and 0.44 (SD = 0.02) MPa for the drained loosely packed, drained densely packed and waterlogged soils, respectively. All bulk soil in the waterlogged root boxes with *R. palustris* and *P. major*, and some of the lower layers of the compacted soils, were blue in colour which indicates a reduced state of the soil.

#### *Gas space formation in compacted and hypoxic soils*

Plants of the three investigated species were grown in PVC boxes ( $40 \times 30 \times 20\text{ cm}$ ) with either ballotini (diameter 6 mm) or quartz sand (diameter 0.32 mm). The space in the boxes was confined by screwing a lid on top, resulting in a constant, small pore diameter in combination with a high mechanical resistance. Nutrients were supplied as a modified, quarter-strength Hoagland solution (Hoagland & Arnon 1950), which was pumped through the boxes at a rate of  $6\text{ litres/h}^{-1}$  and collected again in a supply vessel of 25 litres. The solution was refreshed twice every week. This solution was either saturated with or depleted of oxygen by pumping air or nitrogen gas through it. Thus, four treatments were applied in total: aeration with large pores, aeration with small pores, hypoxia with large pores and hypoxia with small pores, with three plants per species per treatment. Temperatures during the 8-h dark, and 16-h light period were  $20$  and  $25^{\circ}\text{C}$ , respectively. After 3 weeks the three thickest roots of each individual plant were sampled. They were imbedded into Spurr-resin (Spurr 1969) and slices were made with the aid of a microtome of the section 0.5–1.0 cm behind the root tip. One slide of each plant was selected to determine the gas space as the fractional root porosity (FRP = percentage of the root-cross sectional area of the whole root occupied by gas space). The length of the longest root was measured for each situation from tip to (tap)root base. These roots were morphologically indistinctive from those used for the fractional root porosity.

#### *Mathematical and statistical analyses*

Per species the effects of the treatment and glass tubes on total root length, shoot dry weight, total root dry weight, number of spikes (only for *P. major* ssp. *major*) and the effect of glass tubes on root length per segment were tested with a two-way ANOVA procedure (Sokal & Rohlf 1981). After combining the results of the boxes with and without glass tubes within each treatment and species, the effects of separate treatments was tested by means of a series of unpaired Student's *t*-tests (Sokal & Rohlf 1981).

The number of root observations was summed for each row of glass tubes and translated into a standardized number of counts (SNC) which estimates the total number of roots crossing the soil monolith at that row by means of the following formula:

$$\text{SNC}_x = N_x \cdot \frac{W_x}{D_T \cdot N_{T_x}} = N_x \cdot \frac{\text{total soil width}}{\text{observed soil width}},$$

in which  $\text{SNC}_x$  is the standardized number of counts in row  $x$ ,  $N_x$  is the number of roots observed in row  $x$ ,  $W_x$  is the width (mm) of the box at row  $x$ ,  $D_T$  is the diameter of a glass tube (12 mm) and  $N_{T_x}$  is the number of glass tubes in row  $x$ .

Linear regression equations per treatment and per species were fitted for the SNC of the last counts for each row against the root length measured in the layer directly on top of that row of glass tubes. All pairs were taken into account in which SNC was not zero, as well as the first pair counted from the top of the box, in which the SNC was zero. Root lengths were calculated with these regression equations for the different sample times and relative extension rates (RER) were calculated per treatment and per species (May *et al.* 1965) using the formula:

$$\text{RER} = \frac{\ln(l_2) - \ln(l_1)}{t_2 - t_1}$$

in which  $l_2$  and  $l_1$  are the root lengths (cm) at day 2 and 1 respectively. The differences in RER between sample time intervals and treatments within species, as well as differences in fractional root porosities between treatments within one species were tested by means of a series of non-parametric Mann–Whitney  $U$ -tests (Sokal & Rohlf 1981).

## RESULTS

### *Validity of root box observations*

The glass tubes had no significant effects on total root length, shoot dry weight, root dry weight, number of spikes or root distribution throughout the soil segments for any of the species. Neither was any interaction found between the treatment and the glass tubes. Therefore, we concluded that the glass tubes did not influence the development of shoot and root systems.

### *Root distribution*

Although for *R. palustris* root length did not differ significantly between the treatments (Table 1), the spatial distribution of the roots at the end of the experiment and the development of root patterns were totally different. Figure 2 shows the outlines of the root systems at different sampling times. The root pattern of *R. palustris* was oriented in a horizontal direction throughout the experiment, whereas *R. acetosa* and *P. major* showed a far more narrow, downwardly directed growth pattern. This is even more obvious in the compacted soils where none of the roots of *R. palustris* reached the bottom of the boxes in contrast to *P. major* and *R. acetosa*. In waterlogged soils the growth pattern of both *P. major* and *R. acetosa* showed an initial decay of the root system. But whereas *P. major* seemed to recuperate from day 35 onwards, *R. acetosa* was unable to produce new, healthy roots within the 23 days of this experimental series. *R. palustris* formed a new root system with thick, secondary laterals in the soil and thin, highly branched roots at the soil–water boundary.

**Table 1.** Mean shoot dry weight (SDW, g), total root length (TRL, m), and root dry weight (RDW, g) for different treatments with *Plantago major* ssp. *major*, *Rumex palustris* and *Rumex acetosa* at the end of the experiment ( $\pm$  SEM,  $n=7-8$ )

	SDW	TRL	RDW
<i>P. major</i> ssp. <i>major</i>			
L	0.59 $\pm$ 0.10 <sup>a</sup>	21.0 $\pm$ 3.2 <sup>a</sup>	0.20 $\pm$ 0.02 <sup>a</sup>
D	0.59 $\pm$ 0.07 <sup>a</sup>	23.0 $\pm$ 1.2 <sup>a</sup>	0.17 $\pm$ 0.02 <sup>a</sup>
W	0.11 $\pm$ 0.03 <sup>b</sup>	2.8 $\pm$ 0.9 <sup>b</sup>	0.04 $\pm$ 0.02 <sup>b</sup>
<i>R. palustris</i>			
L	2.38 $\pm$ 0.87 <sup>a</sup>	107.5 $\pm$ 16.2 <sup>a</sup>	0.91 $\pm$ 0.15 <sup>a</sup>
D	0.90 $\pm$ 0.38 <sup>b</sup>	66.4 $\pm$ 10.5 <sup>a</sup>	0.67 $\pm$ 0.14 <sup>ab</sup>
W	0.56 $\pm$ 0.19 <sup>b</sup>	95.6 $\pm$ 23.1 <sup>a</sup>	0.38 $\pm$ 0.09 <sup>b</sup>
<i>R. acetosa</i>			
L	0.10 $\pm$ 0.02 <sup>a</sup>	7.0 $\pm$ 0.64 <sup>a</sup>	0.03 $\pm$ <0.01 <sup>a</sup>
D	0.12 $\pm$ 0.01 <sup>a</sup>	6.3 $\pm$ 0.32 <sup>a</sup>	0.03 $\pm$ <0.01 <sup>a</sup>
W	0.03 $\pm$ <0.01 <sup>b</sup>	0.4 $\pm$ 0.12 <sup>b</sup>	<0.01 $\pm$ <0.01 <sup>b</sup>

L=drained, loosely packed, D=drained, densely packed- and W=waterlogged soils).

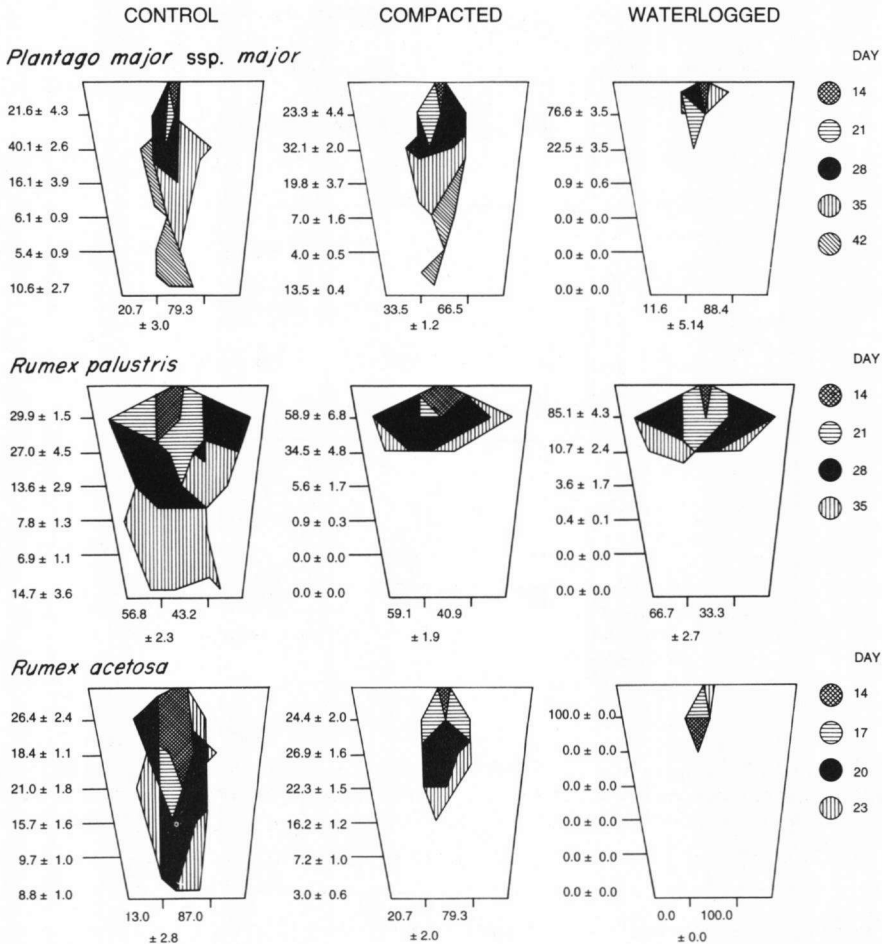
Different letters indicate significant differences in means between treatments within species ( $P \leq 0.05$ ).

### Root growth and decay

The RERs, as calculated by using significant regression equations (SNC  $\times$  measured root length,  $P \leq 0.05$ ), are presented in Fig. 3. In the waterlogged situation, *R. acetosa* did not have enough soil layers with roots to produce a reliable regression equation. For *P. major*, in the waterlogged series, a large part of the root system died soon after waterlogging, resulting in a negative RER; RER became positive again from day 28 onwards. The RER for different treatments of *R. palustris* did not differ very much during the experiment, with the exception of days 21–28 for the drained, loosely packed series. For *R. acetosa* RER in loosely packed soil was significantly lower than that in densely packed soil from day 17 onwards.

### Porosity in roots from compacted and/or hypoxic soils

The formation of gas-space in the roots tips is presented in Table 2 as the FRP. In *R. palustris* and, to a far lesser extent, *R. acetosa* and *P. major*, hypoxia induced the formation of more gas space compared to the aerated situation when grown in a substrate with a large pore diameter. When the pore diameter was small the formation of extra gas space under hypoxic conditions was inhibited in the case of both *Rumex* species. A small pore diameter did not seem to influence the FRP by itself. *R. palustris* showed the largest decrease in root length as a result of small soil pore diameter, followed by *R. acetosa* and *P. major*, respectively (Table 3). *R. palustris* was the only species in which hypoxia in combination with a small soil pore diameter reduced the root length even more compared to the aerated substrate with a small diameter. Root length seemed to increase as a result of hypoxia when the soil pores were large for all three species. But only for *R. palustris* was this increase significant.



**Fig. 2.** Outline of the root systems of *Plantago major ssp. major*, *R. palustris* and *R. acetosa* in a drained, loosely packed (control), drained densely packed and waterlogged soil at different sample times. Percentages of horizontal and vertical distribution of the measured root length at the end of the experiment are also indicated ( $\pm 1$  SEM,  $n = 7-8$ ). Outlines are derived by connecting the glass tubes in which at least two (out of four) replicate boxes per species and treatment scored a root observation. Waterlogging started on days 21, 14 and 14 for *P. major*, *R. palustris* and *R. acetosa*, respectively.

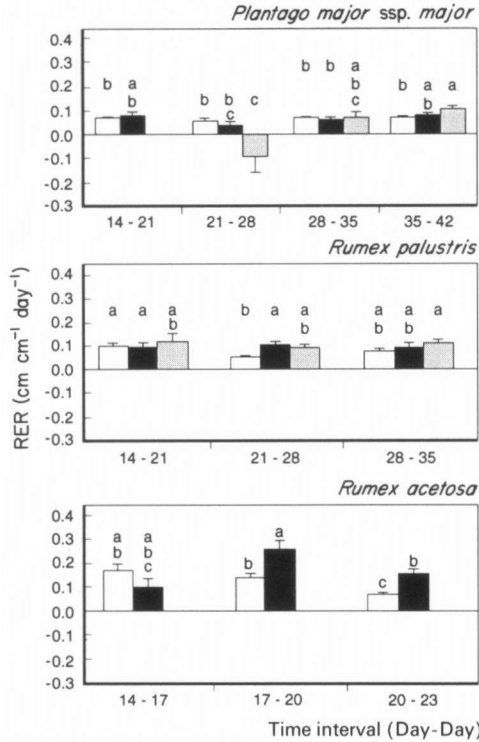
**DISCUSSION**

*Validity of the method*

The modifications of the perforated soil system met the needs of our experiment and proved to be a suitable method to study root architecture under experimental conditions in compacted or waterlogged soil. However, roots growing at the surface, like those in the top layers of the waterlogged boxes with *R. palustris*, cannot be counted with this method and must be quantified separately, for instance by placing a grid on top of the soil and scoring the number of intercepts as described by Newman (1966).

*Root pattern per species*

The downwardly oriented root growth of *P. major ssp. major* and *R. acetosa* in drained soils (Fig. 2) may help to avoid competition with shallow rooted plants for nutrients



**Fig. 3.** Mean relative extension rates ( $\pm 1$  SEM) for *Plantago major ssp. major*, *Rumex palustris* and *Rumex acetosa* in a drained, loosely packed (control, □), drained densely packed (■) and waterlogged (▣) soil at different time intervals, as calculated with the aid of linear regression equations ( $n=4$ ). Different letters indicate significant differences within one species ( $P \leq 0.05$ ).

**Table 2.** Mean fractional root porosity ( $\pm 1$  SEM,  $n=3-4$ ) as a percentage of the root cross-sectional area of the whole root occupied by gas space. Plants of *P. major ssp. major*, *R. palustris* and *R. acetosa* were grown on a substrate with either large or small pore diameter, which was supplied with nutrient solution saturated either with air or nitrogen gas

	Ballotini (6 mm)		Quartz sand (0.32 mm)	
	Aerated	Hypoxic	Aerated	Hypoxic
<i>P. major ssp. major</i>	3.1 $\pm$ 1.1 <sup>a</sup>	6.7 $\pm$ 0.68 <sup>b</sup>	6.2 $\pm$ 2.1 <sup>b</sup>	5.7 $\pm$ 0.06 <sup>b</sup>
<i>R. palustris</i>	5.3 $\pm$ 1.1 <sup>a</sup>	25.7 $\pm$ 1.1 <sup>b</sup>	4.5 $\pm$ 0.65 <sup>a</sup>	2.6 $\pm$ 1.3 <sup>a</sup>
<i>R. acetosa</i>	0.33 $\pm$ 0.12 <sup>a</sup>	2.5 $\pm$ 0.18 <sup>b</sup>	0.53 $\pm$ 0.43 <sup>a</sup>	0.61 $\pm$ 0.35 <sup>a</sup>

Different letters indicate significant differences within one species ( $P \leq 0.10$ ).

and/or water (Berendse 1982) or even physical space (McConnaughay & Bazzaz 1991). Deep root patterns are typical for plants found on higher grounds that can be faced with periods of drought and low soil water tables. In contrast, *R. palustris* showed a more horizontally growing root system, which was observed before (Voesenek & Blom 1987).



**Table 3.** Mean length of roots ( $n=3-4$ ) from root tip to (tap)root base as percentage of the length of roots grown in aerated nutrient solution on 6 mm ballotini. Plants of *P. major* ssp. *major*, *R. palustris* and *R. acetosa* were grown on a substrate with either large or small pore diameter, which was supplied with nutrient solution saturated either with air or nitrogen gas

	Ballotini (6 mm)		Quartz sand (0.32 mm)	
	Aerated	Hypoxic	Aerated	Hypoxic
<i>P. major</i> ssp. <i>major</i>	100 <sup>a</sup>	104 <sup>a</sup>	77 <sup>b</sup>	82 <sup>b</sup>
<i>R. palustris</i>	100 <sup>a</sup>	116 <sup>b</sup>	57 <sup>c</sup>	48 <sup>d</sup>
<i>R. acetosa</i>	100 <sup>a</sup>	110 <sup>a</sup>	61 <sup>b</sup>	57 <sup>b</sup>

Different letters indicate significant differences within one species ( $P \leq 0.10$ ).

### *Waterlogging effects*

Upon waterlogging, *R. acetosa* showed a major decline in shoot dry weight, total root length and root dry weight (Table 1) and a rapid decay of the root system. At first, *P. major* ssp. *major* also showed an enormous setback as a result of waterlogging, but towards the end of the experiment the plants recovered (Figs 2 and 3). Still, all measured growth parameters were significantly lower than those in the control series. The percentage decline in shoot dry weight after waterlogging, relative to the control series, may have been equally high for *R. palustris* as for the other two species, but in contrast to the other two species its shoots looked very healthy and a new superficially growing root system had formed (see also Voesenek *et al.* 1989). Many wetland species possess such a superficially growing root system (Dumortier 1991), thus avoiding the deeper more reduced soil layers (Etherington 1983). The ability of *R. palustris* to penetrate relatively deep into the waterlogged soils (Fig. 2) is probably the result of the ability to form aerenchymatous laterals as long as this is not limited by pore size (Table 2). Root extension in waterlogged soils was largest for *R. palustris*, followed by *P. major* and *R. acetosa*, respectively (Fig. 3). The fractional root porosity in hypoxic, uncompacted soils showed an identical order (Table 2).

### *Compaction effects*

In a field situation, soil compaction may be accompanied by anaerobiosis of the soil, especially under wet conditions (Boone *et al.* 1986) as might be the case directly after a period of flooding. It is not very likely, however, that anaerobiosis influenced root growth in our compacted soils because *P. major* and *R. acetosa* penetrated much deeper into the compacted soil than in waterlogged series.

The influence of compaction on the horizontal redistribution of the roots is, although small, more obvious for *R. acetosa* than for *P. major*. Soil compaction had a far greater negative impact on *R. palustris* (Fig. 2).

Figure 3 shows that in the later sampling periods the relative extension of both *Rumex* species was significantly higher in the compacted soils than in the loosely packed soils. As the root system was not significantly larger in the destructive sampling (Table 1), a larger root system must already have been present in the loosely packed series at the start of the measurements. Thus, root growth was affected most by soil compaction in the early stages of development. The cause for this temporal difference in response to soil compaction is

probably related to the physical state of the top soil. This top soil has a lower water content due to evaporation. As the water content of a soil decreases its mechanical resistance generally increases (Bennie & Burger 1988; Borchert & Graf 1988). The difficulties some species have in penetrating a compacted top soil is well illustrated by Blom (1978). The fractional root porosities of individual roots of the *Rumex* species were unaffected by a small pore diameter itself, but, small soil pores did inhibit the formation of gas space under hypoxic conditions (Table 2). Under waterlogged conditions laterals of *R. palustris* possess many large pores. This adaptation to waterlogging may become disadvantageous in the field directly after a flooding, as the water regresses and the soil becomes more compacted. The structure of the aerenchymatous laterals may then collapse under the external pressure, thus reducing the amount of functional root tissue. This might explain why *R. palustris* is mainly to be found on wet sites. *P. major* ssp. *major* occurs on compacted soils. Our results show its ability to occur on waterlogged soils in the established phase. In waterlogged soil, this species is able to produce new roots, in which the fractional root porosity is unaffected by a small, confined pore diameter. That this species does not occur very regularly on low, frequently flooded sites must be explained by its susceptibility to such conditions during germination and establishment (Blom 1978). Finally, although *R. acetosa* does produce roots with a slightly increased fractional root porosity under hypoxic conditions, this species was unable to maintain its root system in a waterlogged soil. This explains its absence on frequently flooded sites.

In conclusion we can, at least partially, explain the field distribution of the investigated species by their root patterns in waterlogged or compacted soils, as a result of their ability to develop porous tissue in newly formed roots. The development of aerenchyma, and consequently root expansion, can be negatively affected by a high mechanical resistance, as was the case for *R. palustris*.

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