Flooding-induced adventitious rooting in *Rumex*: morphology and development in an ecological perspective

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SUMMARY

The formation of aerenchymatous adventitious roots is a morphological acclimation to soil flooding in many wetland plants. The large air spaces in these roots facilitate the diffusion of gases between shoot and root. This study investigated adventitious root formation in species of the genus *Rumex*, and related the differences between species to the natural habitat of the species.

Large differences in both the number and the morphology of the adventitious roots were found between closely related species. *R. hydrolapathum*, a species of almost permanently waterlogged soils, showed only a slow growth of adventitious roots, but these roots were extremely porous and very thick. *R. palustris*, which is flooded very frequently but not permanently, developed a large number of adventitious roots with a high content of aerenchyma. On the other hand, adventitious rooting in *R. thyrsiflorus* and *R. acetosa*, which are species of dry and seldom flooded habitats, was rather poor and the adventitious roots contained only very little air space. A group of species occurring in regularly flooded grasslands (*R. crispus, R. conglomeratus* and *R. obtusifolius*) showed an intermediate response to soil flooding.

Two contrasting species, *R. palustris* and *R. thyrsiflorus*, showed emergence of adventitious roots within 2 days after the onset of waterlogging. Although the time of onset of adventitious rooting was similar in these two species, the primary lateral root system of *R. palustris* was completely replaced by adventitious roots in 1 week, independently of the age of the plants. In contrast, the biomass of adventitious roots in *R. thyrsiflorus* after 1 week of flooding was never more than one-third of the biomass of the primary lateral root system. We concluded that the ability of species to form adventitious roots during flooded soil conditions and the adaptive characteristics of these roots were very closely related to the flooding frequency of these species in their natural habitat. Differences in adventitious rooting between species mainly occurred in the number, growth rate, morphology and anatomy of the roots, and not in the timing of emergence.

INTRODUCTION

Adventitious rooting in plants has long been recognized as a response to survive prolonged periods of soil flooding or waterlogging (Kramer 1951, reviewed by Jackson & Drew 1984). During waterlogging, the functional root system of most wetland species consists mainly of adventitious roots, which have a low internal resistance to gas diffusion. The presence of longitudinal aerenchyma channels facilitates oxygen diffusion from shoot to root tips (Armstrong 1979; Gaynard & Armstrong 1987; Bedford *et al.* 1991). Soil oxygen concentrations decrease very rapidly upon waterlogging (Ishii & Kadoya 1991), and this adaptive root morphology effectively prevents anoxia stress in the adventitious part of the root system, thereby minimizing the negative effects on plant growth (Kramer 1951; Aloni & Rosenshtein 1982). However, to ensure rapid replacement of the non-aerenchymatous primary roots during waterlogging, adventitious roots have to develop very fast. In experiments of Kramer (1951) and Jackson (1955) with tomato plants, adventitious roots were found after 3–4 days of waterlogging. Wample & Reid (1978) observed the first adventitious root initials in sunflower plants as early as 24 h after the onset of waterlogging, and actual root emergence after 2 days. These experiments concerned crop species, of which the physiology is different from wetland plants. However, a typical wetland species like *Typha* also formed adventitious roots 2 days after the onset of waterlogging (Seago & Marsh 1989).

Justin & Armstrong (1987) have extensively examined the relation between the habitat of a species and the adaptations in roots formed during waterlogging. They found a strong increase in porosity, indicating the formation of aerenchymatous tissue, in the roots of many wetland plants upon soil flooding, whereas roots of non-wetland plants almost without exception maintained very low porosities. Unfortunately, due to the large number of species, only anatomical characteristics could be studied in their paper. It is however likely that not only root porosity, but also number, diameter and rate of development of the adaptive roots determine the waterlogging resistance of a plant species. Our aim was to investigate all these developmental aspects of the formation of adventitious roots.

A very suitable group of species for flooding research is found in the genus *Rumex*. The habitats of the different *Rumex* species range from wet mudflats to dry sandy river dune. Previous investigations with some species of this genus have shown that flooding-resistant species occur in the lower, often flooded parts of the floodplains, whereas intolerant species are mainly found in highly elevated grasslands (Blom *et al.* 1994). Many flooding-related studies on this genus focus on shoot elongation under water, which enables the plant to restore contact with the atmosphere after submergence (e.g. Voesenek *et al.* 1990, 1993). Several adaptations of the root system to flooding have also been described (Laan *et al.* 1989a,b, 1990).

The aim of this investigation was to determine both the anatomical and morphological properties as well as the developmental aspects of adventitious rooting during waterlogging in a wide range of *Rumex* species. This allowed us to draw conclusions concerning a causal relationship between the habitat preference of floodplain species in a hydrological gradient and the characteristics of the adventitious root system these species develop upon flooding. Within this framework, the early stages of adventitious

Table 1. Hydrological characteristics of the habitats of eight *Rumex* species, occurring in the floodplains of the river Waal near Nijmegen (The Netherlands)

| Species | Habitat | Floodplain elevation | Flooding conditions | | Soil moisture |
			Frequency	Duration	
R. thyrsiflorus	Grassland on sand	High	Occasional	Short	Very dry
R. acetosa	Grassland on clay	High	Occasional	Short	Very dry
R. sanguineus	Woodland	High	Occasional	Short	Moist–dry
R. obtusifolius	Flooded grassland	Intermediate	Frequent	Short–intermediate	Moist–dry
R. crispus	Flooded grassland	Intermediate	Very frequent	Intermediate	Wet–dry
R. conglomeratus	Flooded grassland	Intermediate	Frequent	Intermediate	Wet–moist
R. palustris	Exposed mudflat	Low	Very frequent	Long	Wet
R. hydrolapathum	Oxbow lake	Low	Frequent	Long	Water–wet

root formation were studied in *R. palustris*, a species that is particularly well-adapted to flooding, and *R. thyrsiflorus*, which is only poorly adapted. Comparison of the number of the newly formed roots and the time and rate of development provided insight into the capacity of these two species to replace the flooding-intolerant primary root system by adventitious roots during waterlogging.

MATERIALS AND METHODS

Natural habitats of the species

The eight *Rumex* species used in the experiments all occur in different habitats in the floodplain area of the river Waal near Nijmegen (The Netherlands). The differences in habitats are mainly based on the hydrological characteristics of these sites (Table 1).

The two species of the driest habitats, *R. thyrsiflorus* Fingerh. and *R. acetosa* L., grow at places with a high elevation compared to the river water level. Plants of these species are rarely flooded, and flooding periods are short. Soil conditions for *R. acetosa* are moister than for *R. thyrsiflorus*, since *R. acetosa* prefers grasslands on clay, whereas *R. thyrsiflorus* mainly grows on well-drained sandy river dunes. *R. sanguineus* L., a third species of seldom flooded habitats, occurs in floodplain woodlands at high elevations. Although quite moist in spring, this shaded habitat can be rather dry in summer.

Three grassland species of river forelands, *R. obtusifolius* L., *R. crispus* L. and *R. conglomeratus* Murray, are found in a zone that is flooded regularly. *R. obtusifolius* appears to prefer the less frequently flooded part of this habitat, whereas *R. crispus* grows in depressions that are submerged more often and for longer periods. *R. conglomeratus* is found at places where the soil is continuously very moist due to seepage water.

R. palustris Sm. grows on mudflats of former channels that are connected with the river. This is a habitat with extreme hydrodynamical characteristics, such as long flooding periods with turbid water. *R. hydrolapathum* Hudson prefers a habitat with a permanently flooded soil and often grows on the wet banks of oxbow lakes. The frequency of total plant submergence in these lakes, which are protected by levees, is lower than on the mudflats where *R. palustris* occurs.

Greenhouse experiments

Seeds of *Rumex acetosa, R. conglomeratus, R. crispus, R. hydrolapathum, R. obtusifolius, R. palustris, R. sanguineus* and *R. thyrsiflorus* were collected in floodplains and on river dikes near Nijmegen (The Netherlands) and sown in Petri dishes on moist filter paper. After 1 week in a climate chamber (16 h light 20 µmol m^{-2} s^{-1} PPFD (Philips TL33, Philips b.v., Eindhoven, The Netherlands), 27°C; 8 h dark, 10°C), the seedlings were transferred to a greenhouse and planted in PVC cylinders (height 400 mm, diameter 120 mm), filled with a homogenous mixture of river sand and loamy clay (1:1, w/w). The soil was kept slightly moist by watering with tap water. Greenhouse conditions were 16 h light (minimum 200 µmol m^{-2} s^{-1} PPFD, maximum 1200 µmol m^{-2} s^{-1} PPFD), 8 h dark and temperatures between 15°C and 25°C.

For the waterlogging treatment, cylinders with mature plants (6–8 months old) were placed in 175-l containers, which were filled with tap water until the water level reached the soil surface of the PVC cylinders. After various periods of waterlogging, plants were harvested by rinsing the soil from the roots. The number of adventitious roots was counted, and the dry weights of the shoot, tap root, primary lateral roots (i.e. lateral roots that are not adventitious roots; see also Laan *et al.* 1989a) and adventitious roots were determined. Adventitious roots were defined as roots which develop 'out of the normal temporal sequence and at an unusual location' (Barlow 1994). In our plants these roots were unbranched, appearing at the base of the shoot or the upper part of the tap root, and therefore clearly distinguishable from primary lateral roots.

Hydroponic experiments

Seeds of the above-mentioned *Rumex* species were sown in flat plastic trays with black polyethylene grains (Lacqtene Low Density grains, Elf Atochem, France), and soaked in a nutrient solution (2 mM $Ca(NO_3)_2$, 1·25 mM K_2SO_4, 0·5 mM $MgSO_4$, 0·5 mM KH_2PO_4 and the micronutrients FeEDTA (90 µM), NaCl (50 µM), H_3BO_3 (25 µM), $MnSO_4$ (2 µM), $ZnSO_4$ (2 µM), $CuSO_4$ (0·5 µM) and H_2MoO_4 (0·5 µM)). The trays were covered with a glass plate and incubated in a climate chamber (16 h light 20 µmol m^{-2} s^{-1} PPFD (Philips TL33, Philips b.v., Eindhoven, The Netherlands), 27°C; 8 h dark, 10°C) for 1 week. The glass plate was then removed and the seedlings were grown for a further 2 weeks in a growth chamber (16 h light 120 µmol m^{-2} s^{-1} PPFD (Philips TL84, Philips b.v., Eindhoven, The Netherlands), 8 h dark; 22°C). Water losses due to evaporation were compensated by daily addition of nutrient solution. Hereafter, seedlings were selected for uniformity and placed on a hydroponic system consisting of three containers of 20 l (six plants in each container). The containers were connected with an aeration vessel of 30 l, in which the nutrient solution was aerated with an air flow of 120 l h^{-1}. The circulation rate of nutrient solution through the containers was 60 l h^{-1} per container.

The responses of *Rumex* plants to waterlogging can be evoked in hydroponic plants by placing these plants on a hypoxic medium (Laan *et al.* 1989a). For the hypoxia treatment, plants were transferred from aerated nutrient solution to a stagnant hypoxic agar solution (0·1% w:w; nutrient concentrations as in the nutrient solution) that had previously been bubbled with nitrogen gas for 16 h. After the treatment, the number of adventitious roots was counted, and the dry weights of the shoot, tap root, primary lateral roots and adventitious roots were determined.

For morphological studies, seedlings of the eight *Rumex* species were grown for 4 or 5 weeks on 20-l containers with nutrient solution, aerated through bubble stones. Half of the number of plants was then placed on a stagnant hypoxic agar solution, as described above, for 10–16 days. Thereafter, the average root diameters of primary lateral roots (first and second order) and adventitious roots were measured microscopically (magnification × 60). The porosities of the different parts of the root system were measured using a pycnometer, according to the method of Jensen *et al.* (1969). Instead of using a maceration procedure, the roots were cut into segments of approximately 20 mm, submerged in water and placed under hypobaric pressure (1·5 kPa) for 10 min in a vacuum desiccator.

RESULTS

All *Rumex* species developed adventitious roots during waterlogged conditions. However, *R. conglomeratus, R. sanguineus* and *R. palustris* developed a considerably larger number of adventitious roots than the other species (Fig. 1a). In terms of biomass, *R. palustris* exceeded all other species by far in adventitious root formation (Fig. 1b). On the other hand, in *R. thyrsiflorus* both the number (Fig. 1a) and the total weight (Fig. 1b) of the adventitious roots were the lowest of all species.

Although root diameters varied considerably between species, the adventitious roots of waterlogged plants were always thicker than the primary lateral roots (data not shown). To investigate root morphology and anatomy in more detail, the porosity (as a measure of aerenchyma formation) and root diameters were measured in hydroponically grown *Rumex* plants under aerated and under waterlogged conditions. The diameter of primary lateral roots during growth under aerated conditions showed clear differences between species (Table 2). Primary lateral roots of *R. hydrolapathum* and *R. palustris* were almost twice as thick as those of *R. conglomeratus* and *R. sanguineus*. In general, primary lateral roots of hydroponically grown plants had a greater diameter than roots of plants grown in soil (data not shown). After 14 days of waterlogging, all species had developed adventitious roots. The differences between species in the diameter of the adventitious roots were even more distinct than the differences between the primary lateral roots (Table 2). Adventitious roots of *R. hydrolapathum* plants grown on hypoxic agar grew as thick as 2·5 mm (average 1·7 mm), whereas *R. acetosa* and *R. thyrsiflorus* mostly developed thin adventitious roots with an average diameter of no more than 0·6 mm. The diameter of adventitious roots in all species, except *R. acetosa* and *R. thyrsiflorus*, was markedly larger than the diameter of the primary laterals (Table 2). Second order lateral roots were invariably very thin (about one-quarter to one-fifth of the diameter of the first order laterals; Table 2).

The porosity of hydroponically grown root systems varied greatly between the species (Table 3). Primary lateral roots of *R. acetosa* and *R. thyrsiflorus* in particular showed extremely low internal gas volumes of 3 and 6%, respectively, whereas the porosity of the other species ranged between 17 and 36%. There was a particularly large difference in porosity between samples taken from the apical unbranched part of the first order primary laterals and samples that included both first and second order primary laterals (Table 3); the small and thin second order lateral roots reduced the average porosity of the total root system severely. This was most evident in *R. sanguineus*, of which the total root porosity was only 10% of the porosity of the first order lateral roots. The porosity of the tap roots was generally rather low in all species and varied between 7 and 16%
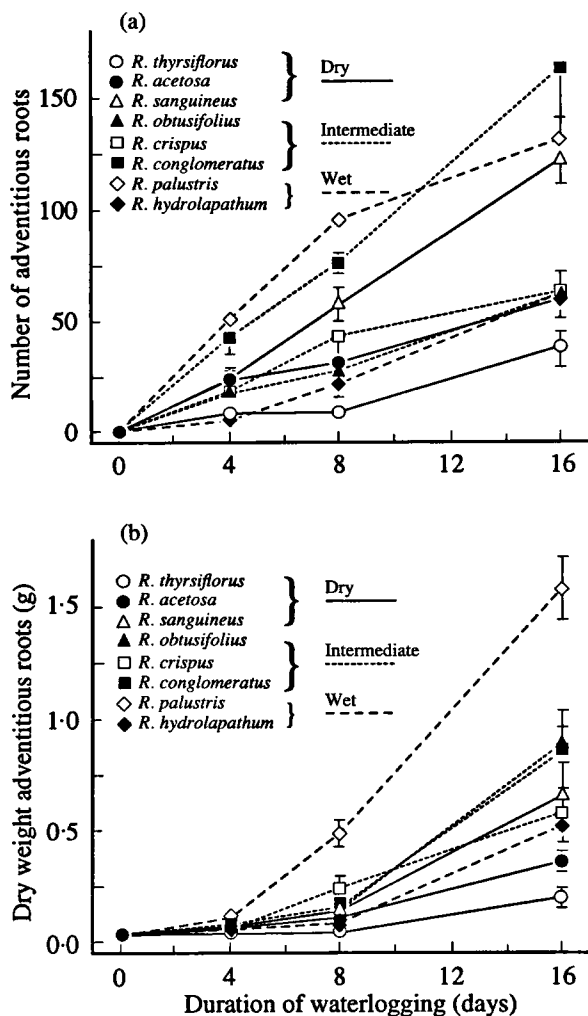
Fig. 1. Number (a) and biomass (b) of the adventitious roots of eight *Rumex* species after various durations of waterlogging. Plants were grown in soil in the greenhouse for 6–8 weeks. Bars indicate SEs; *n*=4.

(Table 3). Adventitious roots of most species showed an approximately 10% (v:v) higher porosity than the primary lateral roots. However, the two species with a very low porosity in the primary laterals, *R. thyrsiflorus* and *R. acetosa*, displayed only a slightly higher internal air volume in the adventitious roots. Also, the porosity of adventitious roots of *R. obtusifolius* did not differ much from the porosity of primary laterals (Table 3), but the volume of air spaces in the primary lateral roots of this species was already relatively high, i.e. 26%.

The development of adventitious roots was fast. Visible roots formed within 4 days of waterlogging in all species (Fig. 1a). Two contrasting species, *R. thyrsiflorus* and *R. palustris*, were compared in more detail in a separate experiment. Within 2 days after the onset of waterlogging, the number of roots of *R. palustris* exceeded adventitious root formation of *R. thyrsiflorus* by far (Fig. 2; note the different *y*-axes for the two species).

Table 2. Diameter of first and second order primary lateral roots and adventitious roots of eight *Rumex* species, grown on hydroponic culture. The natural habitat characteristics are summarized as: Dry, well aerated soil, rarely flooded; Int, moist to wet soil, flooded more or less frequently; Wet, wet to waterlogged soil, flooded frequently to very frequently. Primary roots were harvested at the age of 7 weeks for *R. conglomeratus, R. crispus, R. hydrolapathum* and *R. palustris*, and 8 weeks for the other species, respectively. Adventitious roots were harvested approximately 2 weeks after transferring the plants to a hypoxic agar solution (0·1%, w/w). SEs are given in parentheses; $n=20$

| Species | Habitat | Root diameter (mm) | | |
| | | Primary lateral roots | | |
		First order	Second order	Adventitious roots
R. thyrsiflorus	Dry	0·62 (0·03)	0·09 (0·01)	0·62 (0·04)
R. acetosa	Dry	0·54 (0·03)	0·10 (0·01)	0·62 (0·04)
R. sanguineus	Dry	0·45 (0·02)	0·13 (0·01)	0·79 (0·04)
R. obtusifolius	Int	0·73 (0·02)	0·17 (0·01)	1·00 (0·07)
R. crispus	Int	0·66 (0·03)	0·18 (0·02)	0·80 (0·03)
R. conglomeratus	Int	0·49 (0·03)	0·08 (0·01)	0·88 (0·03)
R. palustris	Wet	0·86 (0·03)	0·20 (0·01)	1·20 (0·06)
R. hydrolapathum	Wet	0·82 (0·03)	0·18 (0·01)	1·73 (0·09)

Table 3. Porosity of first order primary lateral roots, the total of the lateral roots, the tap root and adventitious roots of eight *Rumex* species, grown on hydroponic culture. The natural habitat characteristics are summarized as: Dry, well aerated soil, rarely flooded; Int, moist to wet soil, flooded more or less frequently; Wet, wet to waterlogged soil, flooded frequently to very frequently. Primary roots were harvested at the age of 7 weeks for *R. conglomeratus, R. crispus, R. hydrolapathum* and *R. palustris*, and 8 weeks for the other species, respectively. Adventitious roots were harvested approximately 2 weeks after transferring the plants to a hypoxic agar solution (0·1%, w/w). SEs are given in parentheses; $n=3$

| Species | Habitat | Porosity (% air volume: root volume) | | | |
		Primary lateral roots (first order)	Total primary lateral root system	Tap root	Adventitious roots
R. thyrsiflorus	Dry	5·8 (2·3)	2·4 (0·4)	14·2 (2·3)	7·5 (0·8)
R. acetosa	Dry	2·9 (0·6)	− 1·2 (2·3)	6·8 (0·1)	9·0 (2·4)
R. sanguineus	Dry	17·4 (3·3)	1·7 (0·3)	12·0 (1·4)	29·8 (1·3)
R. obtusifolius	Int	25·6 (3·1)	9·6 (1·8)	12·0 (1·2)	28·8 (0·5)
R. crispus	Int	27·8 (0·4)	15·5 (1·2)	13·9 (1·7)	39·0 (0·1)
R. conglomeratus	Int	28·4 (1·6)	7·2 (1·7)	6·9 (1·1)	41·9 (2·1)
R. palustris	Wet	24·4 (0·9)	8·7 (1·4)	15·5 (1·4)	36·5 (0·5)
R. hydrolapathum	Wet	36·2 (0·7)	17·5 (0·5)	10·0 (2·2)	47·0 (0·3)

However, the timing of first root development (occurring after 1–1·5 days) and the further relative increase in the number of roots was similar in both species.

The differences in the number of adventitious roots between these two species may be explained on the basis of a difference in biomass production of the shoot and/or roots, since the relative growth rate was greater in *R. palustris* than in *R. thyrsiflorus*. To exclude this biomass effect, adventitious root formation in plants of different ages was
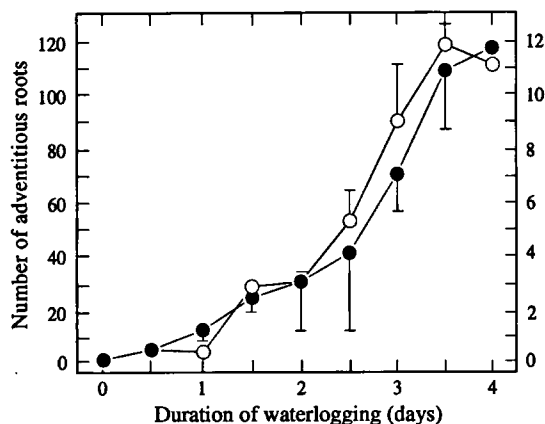
Fig. 2. Number of adventitious roots of *R. palustris* (○) and *R. thyrsiflorus* (●) after various durations of waterlogging. Left axis: *R. palustris*; right axis: *R. thyrsiflorus*. Plants were grown in soil in the greenhouse for 6 (*R. palustris*) or 8 weeks (*R. thyrsiflorus*). Bars indicate SEs; $n=4$.

compared. These experiments showed that the number of adventitious roots increased with increasing age (and size) of the plants, but *R. palustris* plants always developed more roots than *R. thyrsiflorus* plants with comparable or even higher dry weights (Fig. 3a and b). For instance, 6·5-week-old *R. thyrsiflorus* plants, weighing twice as much as 4·5-week-old *R. palustris* plants, formed only half the number of adventitious roots the *R. palustris* plants developed after 1 week of waterlogging. Table 4 shows that in *R. palustris* the biomass of the adventitious roots already equalled the weight of the primary lateral roots 1 week after the onset of the hypoxia treatment. In *R. thyrsiflorus* the biomass of adventitious roots reached only up to one-fifth to one-third of the weight of the primary laterals. Growth of primary lateral roots ceased during hypoxic conditions, as shown by the similar dry weight at the beginning and end of the hypoxic treatment (Table 4).

DISCUSSION

Differences between *Rumex* species in number, biomass, morphology and anatomy of adventitious roots formed upon waterlogging showed to be well correlated to the distribution of these species in the field. *R. palustris* and *R. hydrolapathum* showed the typical aerenchymatous root structure of flooding-adapted plant species. Aerenchyma in the adventitious roots of *R. hypolapathum* was particularly well developed, as indicated by the porosity of 47% (Table 3), which closely resembles the porosities of other true wetland plants like *Typha, Carex* and *Eriophorum* species (Justin & Armstrong 1987; Bedford *et al.* 1991). The porosity of adventitious roots of *R. palustris* was lower, but still high compared to species of seldom flooded habitats (Table 3). Also, the large diameters of both adventitious and primary roots of the two wetland species (Table 2) indicate a high resistance of these roots to soil anoxia. An increased diameter of the root decreases the relative radial oxygen loss to the rhizosphere and therefore enhances oxygen diffusion to the root tip (Armstrong 1979).

Developing high numbers of adventitious roots might be of great importance in surviving waterlogged conditions. *R. palustris* produced a much larger quantity (both
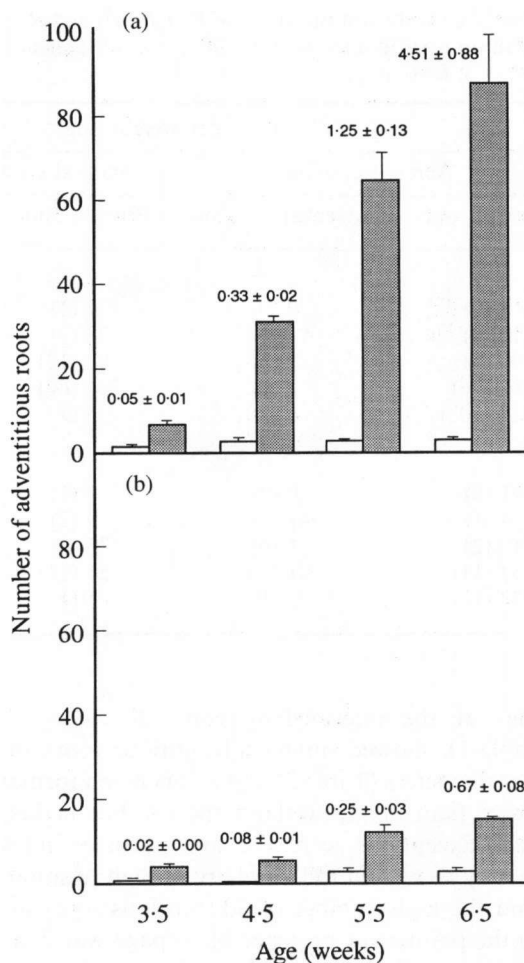
Fig. 3. Number of adventitious roots in *R. palustris* (a) and *R. thyrsiflorus* (b) plants after various durations of aerated growth (open columns) and after one additional week on a stagnant hypoxic agar solution (filled columns). The average plant weight (g) at the end of the hypoxic treatments is shown above each column (± SEs). Bars indicate SEs of the number of roots; $n=6$.

in number and biomass) of adventitious roots than *R. hydrolapathum* (Fig 1a and b). This was mainly due to the lower growth rate of *R. hydrolapathum* roots. Still, *R. hydrolapathum* attained the greatest root length (per root) of all species during waterlogging (data not shown). The difference in kinetics of adventitious root formation between these two species corresponds well with the contrasting hydrological dynamics in the natural habitats (Table 1). *R. hydrolapathum*, growing under permanently waterlogged conditions, survives completely on its aerenchymatous adventitious root system. Though growing slowly during the phase of plant establishment, these roots remain present during the entire life cycle. Water levels in the habitat of *R. palustris* fluctuate much more. This species demonstrates good adaptation to these changes and shows a highly plastic response, maintaining a primary root system with a fairly low porosity during drained conditions, while during a flooding period these roots are rapidly replaced by fast-growing adventitious roots.

Table 4. Biomass of primary and adventitious roots of *R. palustris* and *R. thyrsiflorus* after various periods of aerated growth on hydroponics with or without a subsequent 1 week hypoxia period. SEs are given in parentheses; $n=6$

	Root dry weight (mg)			
Duration of	Aerated growth		Aerated growth + 1 week hypoxia	
aerated growth	Primary roots	Adventitious roots	Primary roots	Adventitious roots
R. palustris				
2·5 weeks	<1 (0)	0 (0)	7 (1)	3 (1)
3·5 weeks	10 (0)	<1 (0)	23 (3)	37 (4)
4·5 weeks	107 (5)	1 (1)	92 (12)	117 (13)
5·5 weeks	283 (26)	2 (1)	303 (60)	179 (30)
6·5 weeks	523 (103)	6 (3)	ND	ND
R. thyrsiflorus				
2·5 weeks	<1 (0)	0 (0)	3 (1)	<1 (0)
3·5 weeks	4 (1)	<1 (0)	9 (2)	3 (1)
4·5 weeks	17 (2)	<1 (0)	23 (2)	7 (1)
5·5 weeks	54 (11)	<1 (0)	56 (11)	10 (1)
6·5 weeks	132 (16)	2 (1)	ND	ND

ND, not determined.

The *Rumex* species of the intermediate zone, *R. obtusifolius*, *R. crispus* and *R. conglomeratus* (Table 1), showed similar adventitious root numbers (Fig. 1a), root biomass (Fig. 1b), root diameters (Table 2) and aerenchyma formation (Table 3), which were generally all lower than in the wetland species, but higher than in the species intolerant to flooding. Exceptions were the low porosity in adventitious roots of *R. obtusifolius*, which may be related to the relatively high position of this species in the intermediate zone, and the high number of adventitious roots in *R. conglomeratus*, a typical adaptation to the permanent presence of seepage water in its habitat.

Adaptive characteristics to alleviate stress from waterlogging were hardly found in the thin (Table 2) and non-aerenchymatous (Table 3) adventitious roots of the two flooding-sensitive species, *R. thyrsiflorus* and *R. acetosa*. The number (Fig. 1a) and biomass (Fig. 1b) of adventitious roots was especially low in *R. thyrsiflorus*, the species of the driest sites. In contrast, the woodland species *R. sanguineus* showed adventitious roots that were thicker and more aerenchymatous than the primary roots, and also the number of adventitious roots was high. However, adventitious roots did not seem to be better adapted to flooding than those of intermediate species, and the major part of the primary root system consisted of very thin second order roots with an almost negligible porosity. A root system mainly consisting of these small branched roots is very unlikely to survive prolonged periods of flooding (Armstrong 1979). Adventitious roots of all the species investigated usually did not develop these second-order branches during our experiments, which adds to the low susceptibility of an adventitious root system to hypoxia stress.

Although the porosity of adventitious roots was always higher than the porosity of the total primary root system (Table 3), the absolute difference seemed to be less in *R. crispus* and *R. hydrolapathum*, in which the primary root systems already showed a high porosity. This corresponds with the trend observed by Justin & Armstrong (1987)

that species with a high porosity during drained conditions usually did not gain much more aerenchyma during waterlogging. In these species, the cortical tissue of the roots might not be able to support a higher volume of air spaces without disturbing the integrity of the aerenchymatous structures. Also, thicker roots will have a very unfavourable surface to volume ratio with respect to water and nutrient uptake. The structure of the aerenchyma in *Rumex* described by Laan *et al.* (1989a) can be classified as a honeycomb-type of air spaces, originating from cells with a cubic radial packing (Justin & Armstrong 1987). Although this structure is quite resistant to pressure from outside, results from Engelaar *et al.* (1993) indicate that compacted soil inhibits the formation of aerenchyma in *Rumex* during hypoxic conditions. This may be the reason that porosities found in our hydroponic experiments tend to be higher than the porosities of soil grown *Rumex* species determined in other studies (Justin & Armstrong 1987; Laan *et al.* 1989a).

The tap root is probably a significant barrier for the diffusion of oxygen from the shoot to the primary roots. This woody tissue had a rather low porosity (Table 3), which explains why adventitious roots mostly developed close to the junction of shoot and tap root. Air channels in the tap root leading to roots at the apical parts of the tap root presumably do not have a sufficiently low diffusion resistance to support these roots during hypoxic conditions.

The fast emergence of adventitious roots upon waterlogging did not appear to be dependent on the flooding resistance of a species (Fig. 1a). Even two contrasting *Rumex* species, the flooding-resistant *R. palustris* and the intolerant *R. thyrsiflorus*, did not differ in the initial development of adventitious roots (Fig. 2), although the absolute number of roots in *R. palustris* was much higher than that in *R. thyrsiflorus*. This difference in number of adventitious roots cannot only be explained by the different size of the plants, because *R. palustris* developed far more adventitious roots than *R. thyrsiflorus* even when plants were of the same size (Fig. 3a and b). This large number of roots in *R. palustris* and the fast growth of these roots assure a rapid substitution of the oxygen-deficient primary root system (Table 4), resulting in an alleviation of flooding stress (Kramer 1951; Sena Gomes & Kozlowski 1980). In contrast, adventitious roots of *R. thyrsiflorus* did not seem to readily replace the primary laterals, since their biomass was still low after 1 week of waterlogging (Table 4). After prolonged waterlogging, this certainly leads to severe nutrient deficiency and decreased shoot growth of the plant (Laan *et al.* 1989b).

We can summarize the results of our experiments as follows:

1. The number and the extent of flooding adapted morphological and anatomical characteristics of adventitious roots that a *Rumex* species develops upon flooding are strongly correlated with the hydrology of its habitat. Species that are often flooded develop large numbers of thick roots with a high porosity, whereas seldom-flooded species generally only form a limited number of poorly adapted adventitious roots.
2. The great numbers and fast growth rate of adventitious roots in *Rumex* species of habitats with a high flooding frequency result in a rapid replacement of the primary root system when waterlogging occurs.

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