

Effects of flooding and trampling on the performance of river foreland species of *Rumex* and *Plantago*

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SUMMARY

The effects of a combined regime of flooding and trampling on survival, growth and reproduction of some species from river forelands, were studied in a large-scale, outdoor experiment. In additional pot experiments, trampling effects were separated into effects of shoot damage and of soil compaction. Resistance of individual leaves to a tearing force and recovery from damage were measured. Species were selected according to their occurrence in the field in relation to trampling and flooding: *Rumex acetosa* from seldom flooded, extensively trampled sites; *R. crispus* from frequently flooded, non-trampled sites; *Plantago major* ssp. *pleiosperma* from regularly flooded, non- to heavily-trampled sites and *P. major* ssp. *major* from seldom flooded, very heavily trampled sites. Only *R. crispus* showed obvious morphological adaptations to flooding but their significance was vastly reduced when flooding was combined with trampling. Although they did not possess any important morphological adaptations, both *Plantago* subspecies survived flooding. Of both *Plantago* subspecies, *P. major* ssp. *pleiosperma* performed better than *P. major* ssp. *major* when soil compaction resulted in hypoxia. *P. major* ssp. *major*, responded better when the major effect was an increase in penetrometer value. *R. acetosa* was negatively affected by trampling, flooding and the combination of both. Flooding inhibited flowering during the experiment and trampling reduced seed production. In the pot experiment no interaction was found between shoot damaging and soil compaction due to trampling. Responses to shoot trampling could largely be explained by the tearing resistance in combination with the recovery characteristics of the species. Species occurring on more trampled sites in the field had a higher resistance to tearing stress and a better recovery after shoot damage.

Key-words: growth, hypoxia, reproduction, shoot damaging, soil compaction.

INTRODUCTION

Flooding and trampling make river forelands highly dynamic ecosystems, with a large spatial and temporal variation in physical and chemical parameters and vegetational composition. Flooding creates a gradient from highly flood-resistant species on low sites

to intolerant species on more elevated places (Blom *et al.* 1990, 1994). Submerged plants are subject to a diminished photosynthetic activity (Nielsen 1993) and to a shortage of oxygen, needed for respiration. Decreased oxygen diffusion combined with respiration of roots and soil organisms results in a hypoxic or anoxic soil (Ponnamperuma 1984). In these soils aerobic processes such as nitrification can no longer take place (Engelaar *et al.* 1991) and are replaced by anaerobic processes such as denitrification, the availability of minerals changes with the redox status of the soil (Laanbroek 1990) and toxic products of anaerobic metabolic pathways can accumulate (Ponnamperuma 1984). Plants occurring on frequently flooded sites have developed different morphological and physiological adaptations. The most widely spread morphological adaptations to inundation are the formation of a root system of superficial roots (Engelaar *et al.* 1993a) and thick lateral roots containing aerenchyma (Laan *et al.* 1991), and a rapid elongation of the shoot (Voeselek *et al.* 1989, 1990). Once the shoot has protruded above the water surface, atmospheric oxygen can reach the root through the leaf, petiole and stem. This oxygen may enable aerobic root respiration, whilst radial oxygen loss along the diffusion pathway creates a small oxidized layer around the root (Laan *et al.* 1989a). Other adaptations include a difference in life history, e.g. the timing of germination and type of seedbank (Voeselek & Blom 1992) and a shorter duration of a plant's life cycle (Van der Sman *et al.* 1993).

Trampling by cattle, humans or machinery affects individual plants and changes the vegetational composition (Edmond 1964; Crawford & Liddle 1977; Blom *et al.* 1979; Ikeda & Okutomi 1992, 1995). Trampling usually results in extensive shoot damage, and causes soil compaction (Liddle & Greig-Smith 1975; Krenzer Jr *et al.* 1989), thus influencing soil physical parameters (Vomocil & Flocker 1961). Depending on soil type and moisture content an increased mechanical resistance to root penetration or soil hypoxia can occur (Bennie & Burger 1988; Boone *et al.* 1986). Increased mechanical resistance has a detrimental effect on root elongation (Bengough & Mullins 1991; Blom 1979; Iijima *et al.* 1991). The effects of hypoxia due to compaction will be similar to those occurring in waterlogged soils. Plants exhibit a number of morphological and physiological adaptations to trampling. The possession of a number of tough or elastic veins (Soekarjo 1992), a high sclerenchyma content (Choong *et al.* 1992), as well as a cryptophytic or prostrate growth form (Warwick 1980) can reduce the effects of trampling on shoots. An increased relative growth rate compensates for the loss of tissue (Oosterheld 1992). Expansion of the root cells in a radial direction results in a thickening just behind the root tip, creating a small void in the soil in front of the root tip. This way the mechanical resistance is reduced, and the root tip can elongate more easily (Hettiaratchi 1990).

Literature on the interactive effects of flooding and trampling by cattle is extremely scarce. Oosterheld & McNaughton (1991), who studied the effects of clipping and trampling on plant growth, argue that a flood-tolerant species should be less tolerant to grazing on an evolutionary scale. However, in their experiments the removal of biomass as a result of the presence of grazers was the only parameter taken into account. For those species which are not preferentially eaten by herbivores, soil compaction, rather than biomass removal, probably plays a key role.

We hypothesize that when a plant is not actually eaten a large part of the impact of cattle is restricted to the root environment. In such cases it is not clear what the major response of a plant to regular floods with intermittent periods of trampling will be.

In this study, in a large-scale outdoor experiment, a number of species and subspecies with known adaptations to flooding or trampling have been screened for their responses to a combined treatment of flooding and trampling, and their responses have been compared with those of a species from occasionally trampled or flooded places. We will attempt to explain the responses of the different species by separating the effects of shoot damage and soil compaction resulting from trampling, and by investigating the resistance of individual leaves to tearing and their recovery from damage.

The species and subspecies selected for this study are: *Rumex crispus* L., a flooding-resistant species from relatively frequently flooded, extensively grazed sites (Blom *et al.* 1990); *Plantago major* ssp. *major* L. from elevated, seldom-flooded sites on and directly along heavily trampled tracks; *Plantago major* ssp. *pleiosperma* Pilger from sites with frequent, long-lasting floods that are non- to intensively grazed (Haeck 1992) and *R. acetosa* L. as a control species from high, seldom-grazed places within the river forelands (Blom *et al.* 1990).

MATERIALS AND METHODS

Preparation

Seeds of *R. crispus*, *R. acetosa*, *P. major* ssp. *major* and *P. major* ssp. *pleiosperma* were collected from river forelands of the Rhine delta area (The Netherlands). They were germinated on moist filter paper in Petri dishes at 10°C during an 8 h dark period and at 25°C (*Rumex* species) and 27°C (*Plantago* subspecies) during the 16 h light period ($10 \mu\text{Einstein s}^{-1} \text{m}^{-2}$). Seedlings at the second leaf stage were used in the experiments.

Soil used in all experiments was a mixture of sieved (mesh size 2 mm), calcareous river sand and air-dried, sandy clay. For the outdoor experiment, per species, 200 large pots (diameter 0.16 m, height 0.50 m) with perforated bottoms were filled with the soil mixture (sand 3: clay 1, v:v). During filling, the soil was compacted twice with a stamper to eliminate large air spaces. For the glasshouse experiments a total of 301 polyethylene pots (diameter 0.13 m, height 0.14 m) were filled with a 1:1 (v:v) mixture of river sand and clay. These pots had four 1-cm diameter holes. Soil loss and root outgrowth through the holes was prevented by a piece of netting (mesh size 50 μm). The soil was saturated with water and compressed by hand. This was repeated after 24 h. Pots were placed in groups of six, on trays filled with tap water (depth 1 cm). A minimum light intensity of $150 \mu\text{E m}^{-2} \text{s}^{-1}$, was supplied by sodium (30 N-T 400W, Philips) and mercury (HLRG, Philips) lamps. The light/dark periods lasted 16 and 8 h respectively, with temperatures of 21–24°C and 18°C.

Trampling and flooding effects

Two series of experiments were conducted outdoors in two large basins. The first series with *R. crispus* and *R. acetosa*, lasted from July 1989 until July 1990. The second series with *P. major* ssp. *major* and *P. major* ssp. *pleiosperma* started in July 1991 and ended in August 1992. Climatological data over the two experimental periods, obtained from the Royal Dutch Meteorological Institute, showed no extreme differences between the two experimental periods.

The prepared pots, each containing two seedlings, were distributed equally over the basins (10 × 6 × 1 m). The floor of the basins was flooded with tap water and the depth of the water was maintained between 5 and 10 cm unless otherwise stated. During the

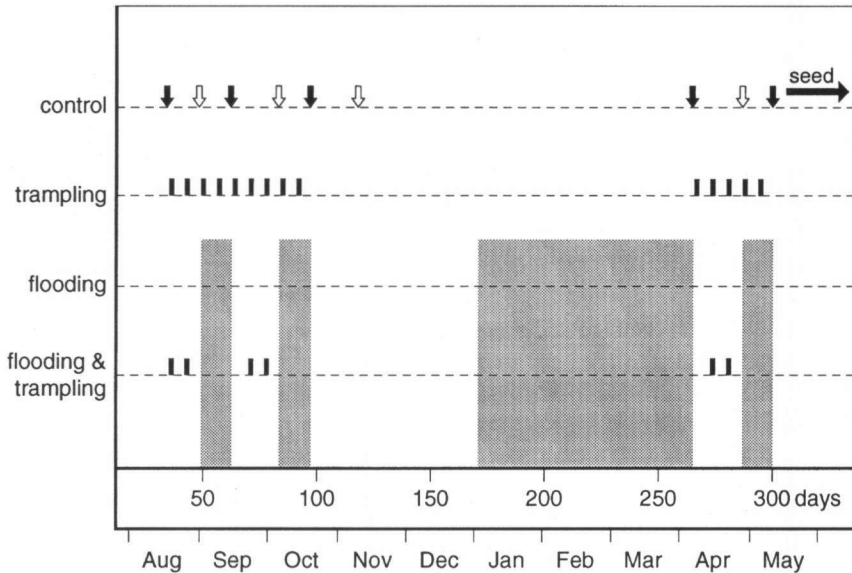


Fig. 1. Schematic presentation of the four treatments in an outdoor experiment during the experimental period. Grey areas represent floods and black bars indicate trampling treatments. Destructive and non-destructive samplings for all four treatments are shown in the control group by closed and open arrows, respectively. Seeds were harvested per plant after the final destructive sampling, as soon as all seeds on that plant had ripened.

first 2 weeks plants were sprayed regularly with tap water. After 2 weeks seedlings were thinned to one per pot. Each species was divided into four groups of 50 plants (Fig. 1). One group served as an untreated control. One group was trampled at intervals of 1 week. The two remaining groups were flooded several times, during which period one of them was trampled in the intermittent non-flooding periods (=combined treatment). Trampling was mimicked by pressing a brass stamper (diameter 0.07 m) on the soil surface, with an applied pressure of 10–13 Mg m⁻². Trampling consisted of pressing the stamper five times, to cover the whole soil surface, and once more directly on top of the plant. Flooding was achieved by filling the basin with tap water, 45 cm over the soil surface. During summer, the water temperature was kept below 25°C by flushing with fresh tap water. During winter the water surface of the basins was occasionally frozen. Flooding or emptying a basin took approximately 10 h.

During the experiment plant survival and reproduction were monitored. Non-destructive sampling was carried out just before flooding of the designated basin and towards the end of the growing season; and destructive sampling at the start of the treatments and after each flood (Fig. 1). At the end of the experiment, some flowering specimens from each series were preserved until the seeds had ripened. Seeds were then harvested and seed quality was determined. In the non-destructive sampling, longest leaf length was measured.

Destructive sampling also included determination of the soil's resistance to penetration, shoot surface area and, after washing, total root length and tap-root dry weight. Shoot surface area and total root length are presented rather than dry weights. This is because they are likely to relate better to functionality, gas exchange, photosynthesis and water and nutrient acquisition of the separate parts. Penetration resistance of the

soil was determined with a penetrometer (conus 3 cm^{-2} , tip angle 60° , Eijkelkamp, The Netherlands) 1 h after the pots were taken out of the basin. Shoot surface area was measured with an area meter (LI-3000, Lambda Instruments, USA) and total root length by means of the line intersect method (Newman 1966) with the aid of a root-length scanner (Comair, Melbourne, Australia). After drying (70°C , 48 h) tap-root dry weight was determined. Total number of seeds per plant was calculated by dividing total seed weight by individual seed weight as determined on a bulk sample of 100 seeds. Seed germination capacity was measured by germinating 150 seeds per plant, as previously described.

Separate and combined effects of shoot and soil trampling

This experiment was conducted in a glasshouse in order to control the environmental conditions as well as possible. To test the influence of trampling on soil parameters, pots without plants were used. The bulk density and percentage pore volume were determined in three pots, using an air pycnometer (Gerhardt, Germany). Pots were trampled twice a week, by pressing a brass stamper (diameter 0.05 m) with a force of $10\text{--}13 \text{ Mg m}^{-2}$, until the entire surface of the soil was trampled. After 2, 6 and 8 weeks, six trampled and six untrampled pots were sampled. Total percentage of pore volume, bulk density, moisture content and percentage of water filled pores were determined in three of the pots. The other three were used for measuring mechanical resistance with a penetrometer (conus 2 cm^{-2} , tip angle 60°). Six pots containing *R. acetosa* plants were used to study the effects of trampling on oxygen availability in the soil in the presence of an oxygen consumer. The soil of these pots was trampled as described above. After 2 and 6 weeks, the redox potential of the soil in these pots was measured 3 cm above the bottom of the pot, using a Pt-electrode in combination with a reference electrode ($\text{Hg}/\text{HgCl}_2/\text{saturated KCl}$, Metrohm, 60701.100) and a mV meter (Metrohm, E488).

Seedlings from each species were individually planted in pots. Treatments started as soon as the plants had reached the exponential growth phase, indicating they were well established. This occurred after 4 or 7 weeks for *Rumex* and *Plantago* species, respectively. At this time six plants of each species were sampled. The remaining plants of each species were then treated according to a two-factorial design: control (no trampling), shoot trampling, soil trampling and combined trampling. Shoots were trampled by pressing the stamper horizontally against the shoot, which was supported by a rubber mat, with a force of $10\text{--}13 \text{ Mg m}^{-2}$. The soil was trampled, without hitting the shoot, as described above. In the combined treatment the shoot and soil were trampled together in a vertical direction. This was done twice a week. Sampling was carried out after 2, and repeated after 8 or 6 weeks for the *Rumex* and *Plantago* species, respectively. At this time some *Plantago* individuals were flowering. These were omitted from the experiment.

Plants were removed from the pots, roots were washed and shoots, lateral roots and tap roots (when present) were separated. Total root length, shoot surface area and tap-root dry weight were measured as described before.

Tearing resistance

From each species, three plants were sampled 6 weeks after potting. The laminae of the youngest full-grown, the oldest and a leaf of intermediate age were cut into pieces ($2\text{--}5 \times 8\text{--}10 \text{ mm}$). Major nerves of the *Plantago* subspecies were sampled separately. The central nerve of *Rumex* leaves was avoided. In contrast to the parallel nerves of

Plantago, it does not give protection to a large part of the lamina. These pieces were placed in two pairs of clamps; one of which was mounted on a movable table, the other was connected to a contractor (25–250 g). By slowly increasing the distance between the clamps a stretching force was applied to the tissue. The tearing force here is defined as the force needed to tear the tissue divided by the width of the piece.

Leaf recovery after damaging

Leaf damage, occurring as a result of the trampling treatments, was imitated by making a sharp fold in the middle of laminae or petioles. For each species, seven plants were used, two of which remained untreated. Of the remaining plants one or two leaves were damaged 5 weeks after potting. The second to fifth youngest leaves were treated. Damage, senescence and recovery of the individual leaves were monitored for 2 weeks. To delay senescence as a result of natural ageing, in week 6 all plants received 2.24 mmol NH_4^+ , 0.98 mmol K^+ , 0.28 mmol H_2PO_4^- and 1.12 mmol SO_4^{2-} . This experiment was repeated twice with three plants from each species, with two being damaged.

Statistical analysis

Before analysing, the length of the longest leaf, total root length, shoot surface area and tap-root dry weight were log-transformed and germination percentages were arcsin transformed. This was done because these biological parameters and ratios often need these transformations in order to show a normal distribution for their data (Sokal & Rohlf 1981). In the outdoor experiment, differences for all parameters within one species and one sampling time between different treatment series were analysed by means of a Tukey procedure (Sokal & Rohlf 1981), significance level 0.05.

In the glasshouse experiment, main treatment effects (shoot trampled and soil trampled) were tested within species and sample time by means of a two-way ANOVA. An additional Tukey procedure was performed to identify the nature of any interaction between the main effects found. Differences in tearing strength between species and age categories of the leaves were analysed with a Tukey procedure. Analysis was performed using the SAS statistical package (SAS Institute Inc., Cary, North Carolina).

RESULTS

Trampling and flooding effects

The penetrometer values of the two series of experiments showed almost exactly the same pattern. The initial value was 0.3–0.4 MPa for all series. As a result of the treatments these values changed until day 97, and remained fairly constant thereafter. The trampled, non-flooded treatment had always a significantly higher value (0.8–1.0 MPa) compared to the other treatments, followed by the trampled, flooded treatment (0.6–0.9 MPa) and, finally, the two untrampled groups which did not differ from each other (0.2–0.4 MPa).

All plants survived the treatments, except for some *R. acetosa* plants from both flooded treatments. For non-sampled plants in these groups, probability of surviving the whole experimental period was 0.35.

R. crispus was the only species with an increase in shoot length large enough to protrude above the water surface during flooding (Table 1). These elongated leaves did not survive very long after the end of a flood. Trampling significantly reduced the

Table 1. Mean length of the longest leaves (cm, ± 1 SEM) of *Rumex crispus*, *Rumex acetosa*, *Plantago major* ssp. *pleiosperma* and *Plantago major* ssp. *major* plants that were trampled, flooded or both, compared to an untrampled, non-flooded control series, at the end of several flooding periods in the outdoor experiment. $n=5$. For *R. crispus* the percentage trampled and untrampled plants that protruded above the water surface during the previous flooding period is given between brackets

Day	62	96	265	300
<i>R. crispus</i>				
Control	17.9 \pm 1.2	18.6 \pm 2.2	15.6 \pm 1.9	20.6 \pm 0.9
Trampled	14.9 \pm 1.2	8.4 \pm 0.7	13.0 \pm 1.1	17.0 \pm 2.5
Flooded	30.3 \pm 3.5 (38)	29.8 \pm 5.2 (0)	38.6 \pm 5.5 (40)	41.2 \pm 6.0 (100)
Both	23.5 \pm 1.8 (2)	15.8 \pm 1.2 (0)	30.7 \pm 2.5 (0)	28.6 \pm 1.5 (0)
<i>R. acetosa</i>				
Control	9.7 \pm 0.7	10.3 \pm 0.8	6.1 \pm 5.2	
Trampled	6.6 \pm 1.2	7.6 \pm 0.4	5.2 \pm 0.9	
Flooded	6.8 \pm 0.7	6.9 \pm 1.2	5.5 \pm 0.3	3.7 \pm 4.5
Both	5.4 \pm 0.4	2.5 \pm 0.2	4.0 \pm 0.3	4.5 \pm 0.3
<i>P. major</i> ssp. <i>pleiosperma</i>				
Control	12.0 \pm 0.5	11.8 \pm 0.4	8.2 \pm 0.7	15.5 \pm 0.6
Trampled	12.0 \pm 0.5	11.0 \pm 0.4	8.5 \pm 0.6	13.6 \pm 0.7
Flooded	14.3 \pm 0.5	14.0 \pm 0.5	15.1 \pm 0.7	18.8 \pm 1.0
Both	13.6 \pm 0.8	13.4 \pm 0.4	10.3 \pm 0.8	17.6 \pm 1.0
<i>P. major</i> ssp. <i>major</i>				
Control	10.5 \pm 0.3	10.8 \pm 0.4	5.8 \pm 0.3	12.6 \pm 0.4
Trampled	12.4 \pm 0.3	11.8 \pm 1.2	6.7 \pm 0.4	12.8 \pm 1.8
Flooded	14.1 \pm 0.5	12.2 \pm 1.0	11.9 \pm 0.6	18.1 \pm 0.9
Both	12.9 \pm 1.0	14.0 \pm 0.9	11.0 \pm 0.5	17.1 \pm 0.7

elongation effect of flooding, both in the number of plants protruding the water surface and the length (Table 1). Both *Plantago* subspecies showed the same tendencies as *R. crispus*, but to a lesser extent. For *R. acetosa* trampling, flooding and the combined treatment significantly reduced longest leaf length compared to the control.

The vegetative growth efforts of the plants in the different treatments are presented in Figs 2, 3 and 4. For *R. acetosa*, the trend was the same for all three parameters. Trampling resulted in a significantly lower shoot surface area and total root length compared to the control. Root length, surface area and dry weight of the tap root of the flooded and the combined treatment were significantly lower than in the non-flooded group. Until day 97, plants in the combined treatment were significantly smaller than those in the flooded treatment (Figs 2, 3 and 4).

After the first flooding, *R. crispus* showed a significantly higher shoot surface area (Fig. 2) accompanied by a significantly lower root length (Fig. 3) and tap-root dry weight (Fig. 4), compared to the control. The second flooding eliminated these differences. Differences in below-ground parameters occurred again after the winter flooding. The shoot surface area of the trampled plants was significantly lower compared to the control treatment at day 97 (Fig. 2). The shoot surface area of the combined treatment did not differ from the trampled plants (Fig. 2) and this treatment

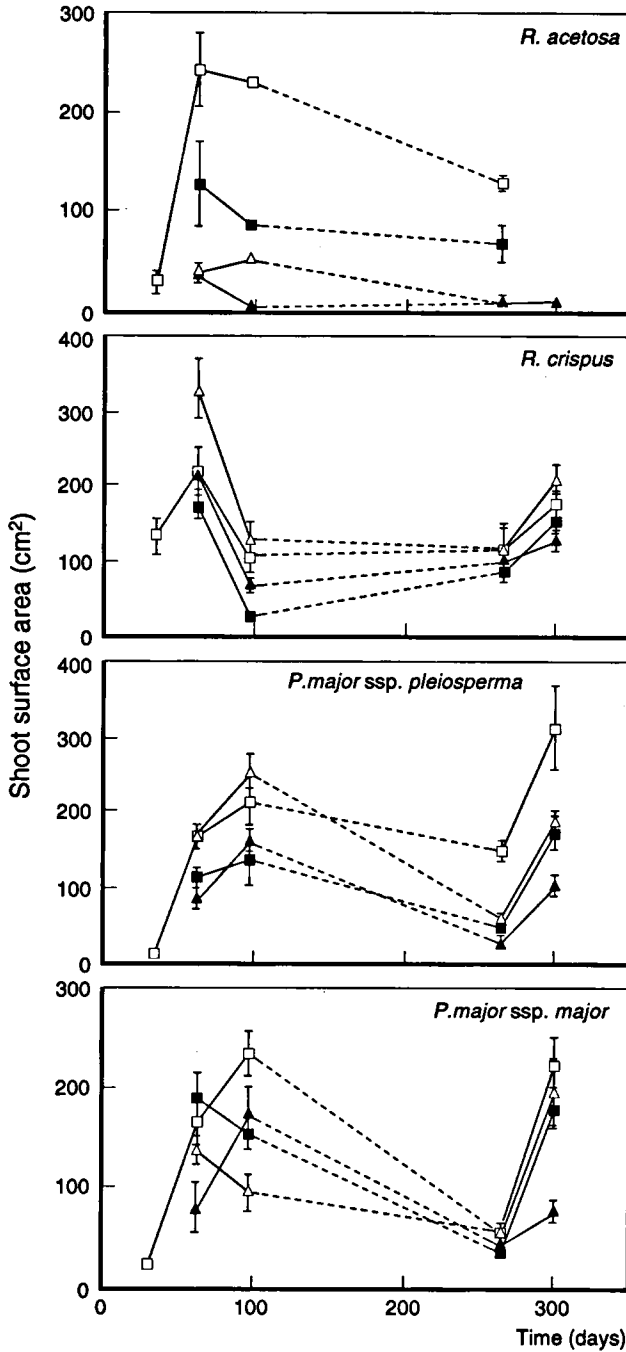


Fig. 2. Mean shoot surface area (cm², ± 1 SEM) of *Rumex crispus*, *Rumex acetosa*, *Plantago major* ssp. *pleiosperma* and *Plantago major* ssp. *major* plants that were trampled (closed squares), flooded (open triangles) or both (closed triangles), compared to an untrampled, non-flooded control (open squares) in an outdoor experiment. $n=5$.

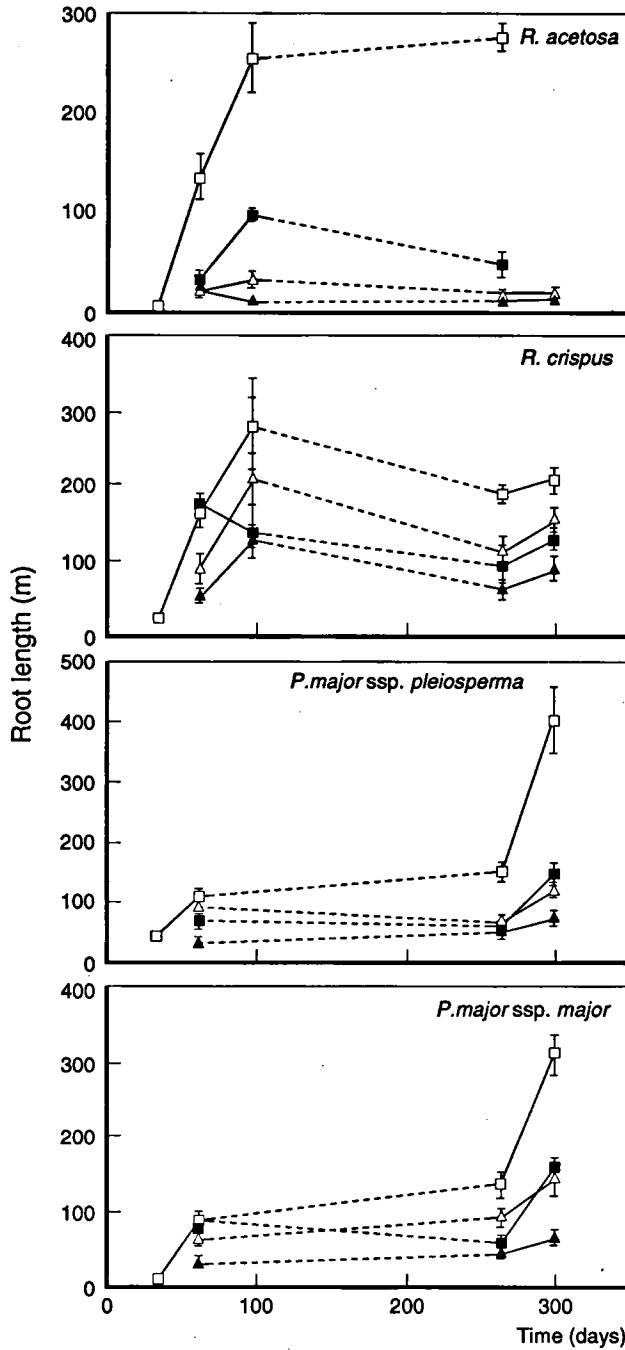


Fig. 3. Mean total root length (m, ± 1 SEM) of *Rumex crispus*, *Rumex acetosa*, *Plantago major* ssp. *pleiosperma* and *Plantago major* ssp. *major* plants that were trampled (closed squares), flooded (open triangles) or both (closed triangles), compared to an untrampled, non-flooded control (open squares) in an outdoor experiment. $n=5$.

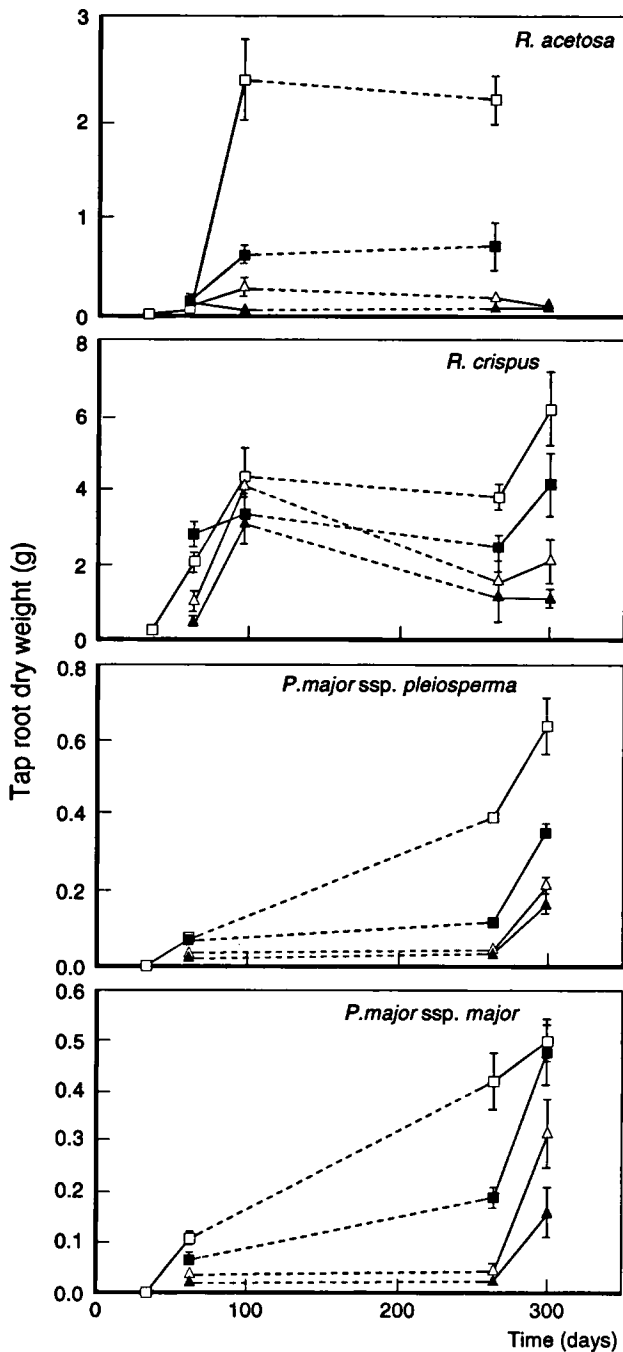


Fig. 4. Mean tap-root dry weight (g, ± 1 SEM) of *Rumex crispus*, *Rumex acetosa*, *Plantago major* ssp. *pleiosperma* and *Plantago major* ssp. *major* plants that were trampled (closed squares), flooded (open triangles) or both (closed triangles), compared to an untrampled, non-flooded control (open squares) in an outdoor experiment. $n=5$.

gave the same results for below-ground parameters (Figs 3 and 4) as the flooded plants, with the exception of the final sampling when the combined treatment had a significantly smaller root length.

In *P. major* ssp. *pleiosperma* the shoot surface area was, when compared to the control series, significantly lower in the trampled and the combined treatment throughout the experiment, and in the flooded treatment in the second growing season (Fig. 2). Compared to the control, root length in this species was significantly lower as a result of trampling and the combined treatment in the first season, and as a result of trampling and flooding in the second season (Fig. 3). At the end of the experiment, plants in the combined treatment had a significantly lower root length compared to the other treatments. Dry weight of the tap root was significantly negatively affected by trampling in the second season, and to an even greater extent by flooding and the combined treatment throughout the experiment.

Compared to the control, shoot surface area of *P. major* ssp. *major* was significantly lower in the trampled and flooded treatments at day 97. The combined treatment showed a significantly lower shoot area and root length than the control, throughout the entire experiment. In the second season, root length in the control group was significantly higher than that in the other three treatments. At the end of the experiment root length in the combined treatment was significantly lower than that in the other groups. The dry weight of the tap roots was significantly reduced by the combined treatment throughout the experiment and by trampling and flooding, except for the last sampling. The flooded and combined treatment series did not differ significantly from each other.

At the end of the first growing season, *P. major* ssp. *pleiosperma* was the only species with a considerable number of flowering plants (day 118, Table 2). The combined treatment of *R. acetosa* was the only series of which no plants flowered at all. In the second growing season, *P. major* ssp. *pleiosperma* produced new spikes throughout a longer period of time than *P. major* ssp. *major*: approximately 2 and 1 month respectively.

Trampled plants of *R. acetosa* produced a significantly smaller number of flower stems (2.4 ± 0.18 ; mean \pm SEM) and ripe seeds compared to the control (4.4 ± 0.83 and Table 2). *R. crispus* always had one flowering stem but the number of seeds produced was significantly highest in the control group (Table 2). The flooded group of *P. major* ssp. *pleiosperma* produced significantly more spikes per plant (11.2 ± 1.2) than the other groups (4.6 – 5.2). Germination capacity was not affected for any of the species by any treatment. For *R. acetosa*, *R. crispus*, *P. major* ssp. *pleiosperma* and *P. major* ssp. *major*, an average of 90, 90, 89 and 100% of the seeds germinated, respectively.

Separate and combined effects of shoot and soil trampling

Bulk density and penetrometer values increased after 2 weeks of trampling (Table 3). In the same period the percentage pore volume decreased by approximately 25%. In the trampled pots, the percentage of waterfilled pores was higher than in the untrampled pots after 2 weeks but lower after 6 and 8 weeks. In untrampled pots the moisture content was very constant from the bottom to the top, but in trampled pots the moisture content was much higher (saturated) in the bottom than in the top soil, where sampling was done. Trampling reduced the redox values of the soil (Table 3).

The effects of trampling on the functional parameters, i.e. shoot surface area and total root length of the four species are illustrated by Figs 5 and 6. Although differences

Table 2. Flowering characteristics of *R. acetosa*, *R. crispus*, *P. major* ssp. *pleiosperma* and *P. major* ssp. *major* plants which were trampled, flooded or both, compared to a non-flooded and untrampled control series in the outdoor experiment. For *P. major* the date of first flowering in the second season is presented. Figures between brackets indicate SEM ($n=5$)

	Plants flowering (%)		Number of seeds per plant	Date of first flowering
	Day 118	Day 365		
<i>R. acetosa</i>				
Control	0	100	1100 (250)	28 March
Trampled	0	100	200 (50)	8 May
Flooded	0	4	80 ($n=1$)	27 June
Both	0	0	0	
<i>R. crispus</i>				
Control	0	100	1700 (100)	25 April
Trampled	0	100	700 (150)	11 April
Flooded	0	100	750 (200)	9 May
Both	0	53	1000 (100)	9 May
<i>P. major</i> ssp. <i>pleiosperma</i>				
Control	60–80	100	16 000 (800)	21 May
Trampled	60–80	100	17 000 (1000)	21 May
Flooded	60–90	100	20 000 (2700)	28 May
Both	60–80	100	19 000 (2000)	28 May
<i>P. major</i> ssp. <i>major</i>				
Control	10–15	100	9100 (900)	17 June
Trampled	10–15	100	6500 (800)	24 June
Flooded	0	100	13 100 (600)	24 June
Both	0	100	8200 (1300)	17 June

between the control and the three trampling treatments were not as large for *R. crispus* as for *R. acetosa*, the two *Rumex* species showed the same patterns. For shoot surface area as well as total root length; shoot trampling gave the smallest reduction followed by soil trampling and total trampling, respectively. This pattern was most obvious after 8 weeks of trampling. This is also reflected by the ANOVA analyses, which show significant effects of shoot and soil trampling for both parameters (Table 4). Soil trampling and total trampling had a devastating effect on *R. acetosa* compared to the control or shoot trampling.

After 8 weeks of trampling, a significant negative effect of soil and shoot trampling on tap-root dry weights of *R. crispus* was found (Tables 4 and 5), as well as a small interaction effect between the two main treatments (Table 4). This effect can be explained as a larger decrease in the combined treatment than would be expected on the basis of the separate treatments. All treatments differed significantly from each other, as determined with a Tukey test. For *R. acetosa* a significant lower tap-root dry weight was found when the soil was trampled compared to the untrampled treatment (Tables 4 and 5). There were no significant tap roots produced by *R. acetosa* after 2 weeks of treatment, nor by both *Plantago* subspecies throughout the entire experiment. In contrast to the *Rumex* species shoot surface area and total root length of both *Plantago* subspecies were unaffected by shoot trampling. But, whereas *P. major* ssp. *pleiosperma*

Table 3. Mean bulk densities (Mg m^{-3}), soil moisture contents (% weight), percentages of pore volume, percentages of waterfilled pores, penetrometer values (MPa) and redox values (mV), all ± 1 SEM ($n=3$), for untrampled soils and soils which were trampled twice a week

	Week			
	0	2	6	8
Untrampled				
Bulk density	1.43 \pm 0.02	1.47 \pm 0.04	1.49 \pm 0.04	1.50 \pm 0.02
Moisture content		15.3 \pm 0.08	14.6 \pm 0.09	14.5 \pm 0.07
Pore volume (%)	42.0 \pm 0.43	41.7 \pm 0.82	40.0 \pm 0.38	39.6 \pm 0.22
Waterfilled pores (%)		70.0 \pm 2.4	68.8 \pm 2.2	70.0 \pm 5.3
Penetrometer value		0.17 \pm 0.01	0.19 \pm 0.01	0.19 \pm 0.01
Redox value		450 \pm 50	420 \pm 40	
Trampled				
Bulk density		1.63 \pm 0.02	1.65 \pm 0.02	1.66 \pm 0.03
Moisture content		14.0 \pm 0.26	10.0 \pm 0.20	10.3 \pm 0.18
Pore volume (%)		34.1 \pm 0.56	33.0 \pm 0.45	33.2 \pm 0.72
Waterfilled pores (%)		82.3 \pm 1.2	60.2 \pm 2.0	61.4 \pm 3.2
Penetrometer value		0.62 \pm 0.05	0.84 \pm 0.10	0.96 \pm 0.02
Redox value		320 \pm 60	150 \pm 10	

Table 4. ANOVA of main treatment effects (shoot trampled, soil trampled) in a glasshouse experiment and their interaction on shoot surface area, total root length and tap-root dry weight of *R. acetosa* (R.a.), *R. crispus* (R.c.), *P. major* ssp. *pleiosperma* (P.m.p.) and *P. major* ssp. *major* (P.m.m.) plants at two different sample times ($n=4-6$)

Week	R.a.		R.c.		P.m.p.		P.m.m.	
	2	8	2	8	2	6	2	6
Shoot surface area								
Shoot	NS	*	NS	***	NS	NS	NS	NS
Soil	NS	***	***	***	NS	NS	NS	**
Interaction	NS	NS	NS	NS	NS	NS	NS	NS
Total root length								
Shoot	NS	*	NS	***	NS	NS	NS	NS
Soil	**	***	NS	***	NS	NS	NS	***
Interaction	NS	NS	NS	NS	NS	NS	*	NS
Tap-root dry weight								
Shoot		NS	NS	***				
Soil		**	NS	***				
Interaction		NS	NS	*				

NS, not significant.

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

also did not show any effects of soil trampling, this treatment significantly decreased the amount of shoot surface area and total root length for *P. major* ssp. *major* (Table 4, Figs 5 and 6).

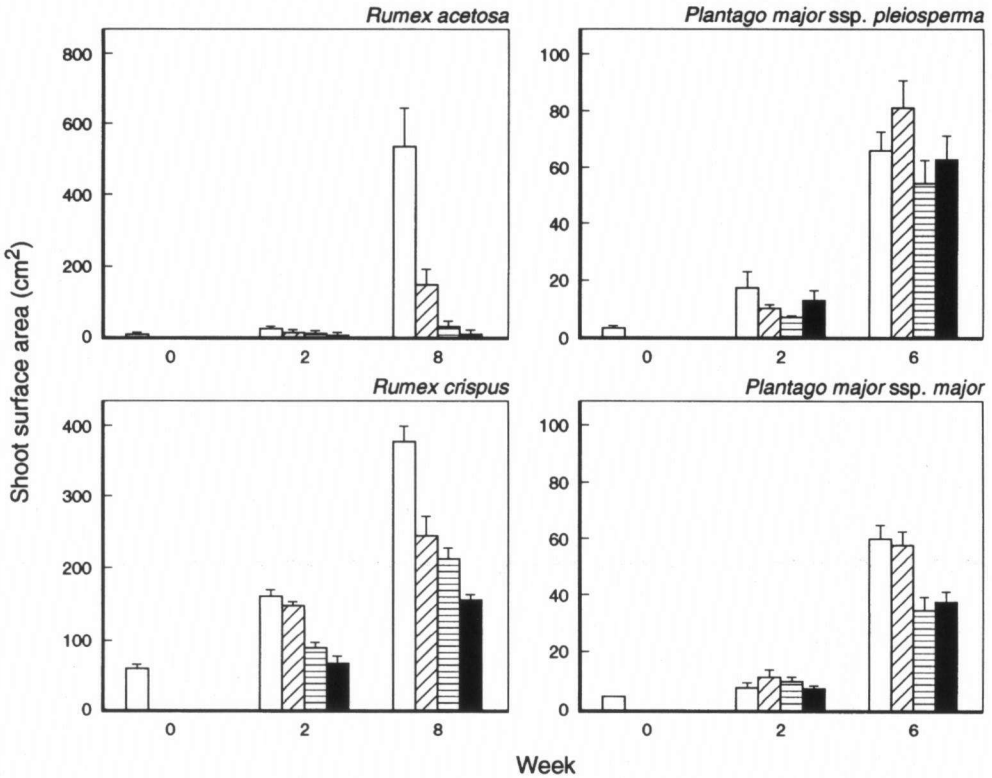


Fig. 5. Mean shoot surface area (cm^2 , +1 SEM) of *Rumex crispus*, *Rumex acetosa*, *Plantago major* ssp. *pleiosperma* and *Plantago major* ssp. *major* plants, grown in a glasshouse, which remained untrampled (open bars) or had their leaves (cross-hatched bars), surrounding soil (horizontally hatched bars) or both (closed bars) trampled twice a week, for 2, 6 or 8 weeks. $n=4-6$.

Tearing resistance

The highest resistance to tearing was found for *R. acetosa*, followed by *P. major* ssp. *major*, *P. major* ssp. *pleiosperma* and *R. crispus*, respectively (Fig. 7). But the lamina of the *Plantago* subspecies has several nerves running parallel from the base to the top of the leaves. In contrast, the *Rumex* species possess a featherlike network originating from one large nerve in the centre of the leaf. The smaller nerves of *R. acetosa* were already included in the tissue samples. Tissue pieces of both *Plantago* subspecies containing a nerve had a significantly higher resistance to tearing than pieces without a nerve. When this was taken into account *P. major* ssp. *major* had a higher resistance than *R. acetosa*. The strength of the main nerves of both *Plantago* subspecies is emphasized by the fact that instead of breaking they were torn out of the laminae, undamaged over several mm.

Leaf recovery after damaging

The response of individual damaged leaves was unaffected by whether or not another leaf on the same plant was damaged. It was obvious that the leaves of the *Plantago* subspecies, particularly *P. major* ssp. *major*, recovered far better than those of the *Rumex* species (Table 6). Both *Plantago* subspecies produced scar tissue at the site of

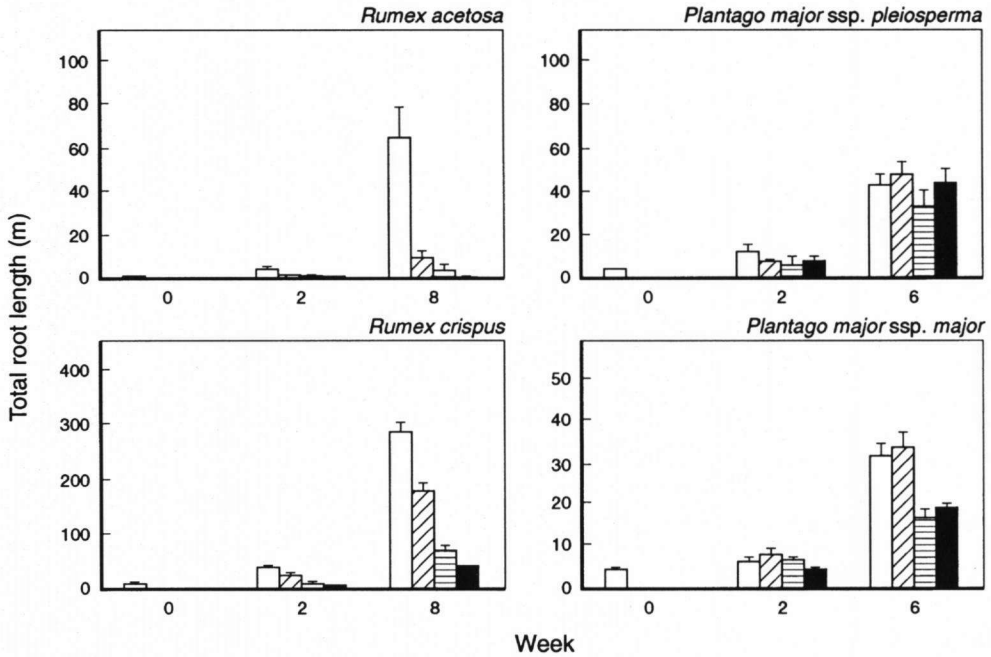


Fig. 6. Mean total root lengths (m, +1 SEM) of *Rumex crispus*, *Rumex acetosa*, *Plantago major ssp. pleiosperma* and *Plantago major ssp. major* plants, grown in a glasshouse, which remained untrampled (open bars) or had their leaves (cross-hatched bars), surrounding soil (horizontally hatched bars) or both (closed bars) trampled twice a week, for 2, 6 or 8 weeks. $n=4-6$.

Table 5. Mean tap-root dry weights (g \pm 1 SEM) of *R. acetosa* and *R. crispus* plants, grown in a glasshouse, which remained untrampled (control) or had their leaves, surrounding soil or both (combined treatment) trampled twice a week for 2 or 8 weeks. $n=5-6$

Week	2	8
<i>R. acetosa</i>		
Control		0.41 \pm 0.17
Leaves		0.12 \pm 0.01
Soil		0.07 \pm 0.02
Combined		0.04 \pm 0.02
<i>R. crispus</i>		
Control	0.15 \pm 0.02	5.68 \pm 0.12
Leaves	0.15 \pm 0.01	4.01 \pm 0.23
Soil	0.22 \pm 0.02	2.54 \pm 0.11
Combined	0.09 \pm 0.02	1.33 \pm 0.16

folding, whereas the *Rumex* species showed deterioration of the surrounding tissue. Also, the leaves of the *Plantago* subspecies grew upright again, in contrast to those of the *Rumex* species.

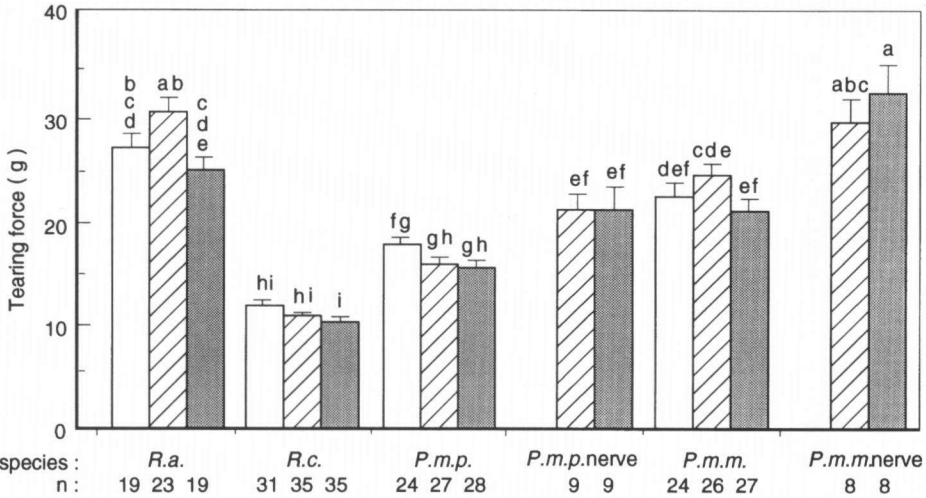


Fig. 7. Mean tearing forces (g, +1 SEM), of the oldest (open bars), an intermediate (cross-hatched bars) and the youngest full-grown (shaded bars) leaf of *Rumex crispus*, *Rumex acetosa*, *Plantago major* ssp. *pleiosperma* and *Plantago major* ssp. *major* plants. Different letters indicate significant differences within one species ($P \leq 0.05$).

Table 6. Morphological changes in leaves of *R. acetosa*, *R. crispus*, *P. major* ssp. *pleiosperma* and *P. major* ssp. *major*, 1, 7 and 14 days after folding of the laminae or petiole. Only differences with leaves on undamaged plants are described. Unless stated differently, observations apply to the leaf parts beyond folding. Different leaf age is indicated with 'I' for the second youngest to 'IV' for the fifth youngest grown leaf

Day	Species	Morphological changes
0	All	Folding of predestined leaves and petioles.
1	All	Brown or black coloration of tissue surrounding the folding.
7	<i>Rumex</i>	Tissue coloration less black or brown.
	<i>Plantago</i>	Tissue coloration returning to green, formation of scar tissue on damaged site.
	<i>R. acetosa</i>	I & II, moderately firm-firm; III & IV, weak-moderately firm.
	<i>R. crispus</i>	I-IV, laminae weak.
	<i>P. m. pleiosperma</i>	I & II, firm; III & IV, moderately firm-firm; when petioles damaged weak.
14	<i>P. m. major</i>	I-IV, firm.
	<i>Rumex</i>	Necrotic spots along the damaged site.
	<i>R. acetosa</i>	I-IV, weak, also before damaged site; 5-8 oldest leaves senescent compared to 0-3 oldest in undamaged plants.
	<i>R. crispus</i>	I & II, weak, green; III & IV, weak, succumbed.
	<i>P. m. pleiosperma</i>	I & II, firm; III & IV, weak-firm, all leaves green, firm leaves upright again.
	<i>P. m. major</i>	I-IV, moderately firm-firm, green, laminae upright again, some with a twist.

DISCUSSION

By restoring contact with the atmosphere (Table 1), *R. crispus* displayed a distinct adaptation to flooding. This species produces aerenchymatous roots when being flooded

or waterlogged (Laan *et al.* 1989b). In this way, atmospheric oxygen is provided to the plant and the rhizosphere. Neither of the *Plantago* subspecies showed any important morphological adaptations to flooding. Possibly they survived flooding by lowering their metabolic activity to a state of virtual 'dormancy', using very little oxygen and carbon reserves (Laan & Blom 1990). Another possibility would be an acceleration of glycolysis in combination with fermentation, using carbohydrates from reserves in the tap root (Jackson & Drew 1984; Voesenek *et al.* 1993). Although *Plantago major* is known to produce large tap roots (Kutschera 1960), in our experiment no large reserves were established (Fig. 4), indicating that this metabolic adaptation could not have played a major role. The production of new spikes throughout a relatively long time period reduces the danger of losing all chance of reproduction as a result of a short stress period. In the field, the relatively long life cycle of *P. major* ssp. *major* compared to *P. major* ssp. *pleiosperma* (Table 2), probably partly explains why it is less often found on frequently flooded sites.

For *R. acetosa*, the effects of trampling were less devastating than those of flooding, but a delay of flowering and a highly diminished seed production (Table 1) may threaten renewal of *R. acetosa* in a trampled area.

Soil compaction often reduces root growth due to increased penetration resistance (Sri Agung & Blair 1989; Bengough & Mullins 1991) in relation with a decreased soil-pore diameter (Moss *et al.* 1988). Hypoxia, as indicated by the low redox potential, probably played a more vital role in the last weeks of the pot experiment. Armstrong (1979) and Ponnampertuma (1984) described hypoxia as a result of water saturation in soils. The decline in air-filled pore volume of the soil results in a decreased gas diffusion (Xu *et al.* 1992), becoming zero even when some air-filled pores, comprising 10% of the soil volume, are still present. The increase in penetrometer resistance (Table 3) for the trampled pots probably relates to the upper parts of the soil. In the deeper soil layers the resistance is likely to have decreased with an increasing soil moisture content (Borchert & Graf 1988). Hypoxia of the soil explains why *R. acetosa* was relatively much more affected by soil compaction in the pot experiment than in the first season of the outdoor experiment, where no signs of hypoxia were found in non-flooded, trampled soil (compare Figs 2, 3 and 4 with Figs 5 and 6). In contrast to *P. major* ssp. *major*, *R. acetosa* failed to develop a healthy root system under waterlogged conditions (see Engelaar *et al.* 1993a). Of the other two species, *R. crispus* is adapted to root hypoxia (Laan *et al.* 1989a,b) whereas *P. major* ssp. *pleiosperma* is known to grow on wet places (Haeck 1992) and should therefore also be adapted to these conditions.

In the outdoor experiment, Both *Plantago* subspecies showed roughly the same responses to trampling as *R. crispus* when considering the vegetative parts, although the *Plantago* subspecies seem to be morphologically better adapted (Kuiper & Bos 1992).

The reactions to combined soil and shoot trampling (Figs 5 and 6) were the sum of the responses to either shoot or soil trampling, as illustrated by the low number of interactions between the main treatments (Table 4). Hence, both *Plantago* subspecies are unaffected by shoot damaging. From the results of the non-flooded, trampled series in the outdoor experiment it then becomes clear that *P. major* ssp. *pleiosperma* is more affected by an increased mechanical resistance of the soil than *P. major* ssp. *major*.

The responses to shoot trampling (Figs 5 and 6) can largely be explained from the tearing resistance (Fig. 7) and recovery after damaging (Table 6). Tearing resistance of *R. acetosa* (Fig. 7) is higher than would be expected by its tolerance to shoot trampling (Figs 5 and 6). *R. acetosa* is, however, the only species in which the life span of an

individual leaf seems to be negatively affected by shoot damaging, even when that particular leaf was not damaged (Table 6). This would ultimately result in a decrease in photosynthetic tissue, with a subsequent delay in production. For both *Plantago* subspecies, the parallel, longitudinal orientation of the nerves, in combination with the presence of adapted cell types and sclerenchyma around the vessels protect the leaf against a large biomass loss and inhibition of transport, which explains why the damaged leaves recovered so well (Soekarjo 1992). The fact that *R. crispus* puts a relatively large effort into its below-ground parts, especially the tap root (Fig. 4), when trampled can also be considered as a good adaptation to above-ground biomass losses.

When flooding and trampling are combined the morphological adaptations of *R. crispus* to flooding become virtually useless, which explains why not all plants were able to complete their life cycle (Table 2). Trampled plants cannot protrude above the water surface (Table 1). The plant will have to rely on photosynthetically derived oxygen for root respiration (Laan *et al.* 1991). Under field conditions this alternative oxygen supply will be hampered when the water has a low light transmission coefficient or when the plants are deeply submerged. The formation of aerenchyma will be inhibited at high soil mechanical resistances (Engelaar *et al.* 1993b) or aerenchymatous roots may be compressed by soil trampling. For species that will be grazed, elongation of the leaves in response to flooding will be disadvantageous, since more biomass will be removed (Ridge 1987; Oosterheld & McNaughton 1991; Van Deursen & Drost 1990).

In contrast to *R. crispus*, all individuals of both *Plantago* subspecies flowered when trampled and flooded. A possible explanation is that in *R. crispus* a certain amount of reserve biomass (tap root) is needed before flowering starts. With the growth of the flowering stem most of the vegetative parts of the shoot die (results not shown). The relatively small amount of photosynthetic active tissue in the flowering stem may not be sufficient to support the production of the generative parts and the seeds. In contrast, the *Plantago* subspecies maintain their vegetative shoots during flowering. The energy and carbon needed for the production of spikes and seeds can be provided for, without relying on reserves already present in a large tap root.

It is obvious that flooding and trampling in the established and generative phase of growth influence the field occurrence of the investigated species. A species with no obvious adaptations of life-history traits nor of morphology such as *R. acetosa*, cannot occur on flooded nor on heavily trampled sites. Therefore, in river forelands this species is found on higher places with a more dense vegetation. In contrast to the other species studied, which occupy gaps in the vegetation, *R. acetosa* would be expected to be a stronger competitor, as indeed was found by Voesenek (1990).

The other species and subspecies, especially both *Plantago* subspecies, are established in gaps in the vegetational cover caused by some environmental parameters. *R. crispus* is well adapted to submergence and thus can claim sites low in the river forelands where many other species are not able to complete their life cycle. Since, the morphological adaptations to flooding displayed by *R. crispus* lose their significance when plants are trampled between floods, this species will only occur on frequently flooded sites when these are not or only lightly trampled.

The *Plantago* subspecies reacted, with exceptions, in a similar way to the treatments, which underlines their close phylogenetic relationship. Both occur on moderately to heavily trampled sites and were not affected by shoot trampling. However, the subspecies occurring on relatively dry places, *P. major* ssp. *major*, seems best adapted to a high mechanical resistance, whereas *P. major* ssp. *major* is the subspecies performing

better under hypoxic conditions. This explains why, compared to *P. major* ssp. *major*, *P. major* ssp. *pleiosperma* inhabits relatively wet sites. As a result of a short life cycle and the vast numbers of seed that are produced, a field population can persist. *P. major* ssp. *major* profits from gaps created by wheel or cattle traffic and is found on and along regularly trampled tracks with a low vegetation. Here, its prostrate growth form will not be a disadvantage with respect to competition for light but it does prevent excessive damage as a result of wear by traffic. In places with a denser vegetation both *Plantago* subspecies would most likely lose to more erect growing species in the competition for light.

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