Introduction and methods

In addition to the study on the influence of trampling and soil compaction on the germination, seedling emergence, and seedling establishment of Plantago lanceolata L., P. coronopus L., P. major L. ssp. major and P. media L. (Blom 1976, 1977, 1978a), experiments were performed to investigate the effects of these two environmental factors on the reaction of full-grown plants. The influence of compaction separately and of trampling and compaction in combination on the diameters of the rosettes of these species has been described in a previous paper (Progress Report 1977). Additional data will be presented in this report.

The study was performed on three series of experimental plots in which seedlings of the four Plantago species were planted in rows in April 1976 (distance between the plants: 15 cm). The sandy soil of the various plots was artificially compacted such that, up to a depth of 1 metre, a moderately and a strongly compacted substrate was created in two series. For purposes of comparison, a loose soil was used in one series of plots.

Trampling was carried out with a trampling machine (see Progress Report 1977). To study the effects of compaction alone and of compaction and trampling in combination, the individual plants of the four species growing in one half of each plot were trampled. The following treatments were applied: light trampling (once a day) on the loose soils, moderate trampling (three times a day) on the moderately compacted soils, and heavy trampling (six times a day) on the strongly compacted substrates.

To investigate the effects of the various treatments on the development of the root systems, in three of the plots (A3, B3, and C3; see Progress Report 1977) the rooting patterns and the biomass distribution in three successive soil layers were determined in September 1977.

The rooting patterns were determined by means of the ‘pinboard’ method (see Schuurman and Goedewaagen 1965). For these measurements, boards covered with steel pins at a distance of 2.5 cm were used. The length of the pins was 10 cm. The two-dimensional contour of the root system of each plant was determined by counting the numbers of pins covered by its roots. In this way the size of the root system of each individual plant was determined. For the determination of biomass, the plants were dried at 70°C for 24 hours. To get an impression of the distribution in the soil, the roots of each plant were harvested in three successive soil layers (0–12.5 cm, 12.5–25 cm, and 25–37.5 cm).

In addition to the measurements of the diameters of the rosettes (Progress Report 1977) in 1977 the numbers of spikes of the plants growing in plots A1, B1, and C1 were determined. Samples were taken to determine the numbers of seed per spike, from which the numbers of seeds per plant were calculated.
The trampling experiments on the remaining plots will be continued until at least the end of 1979.

Results

Rooting patterns

The shape of the root systems of the four *Plantago* species in the six treatments is indicated by the outlines in Fig. 7.2.1. For all species studied, the largest root systems occurred in the untrampled loose soils. In these substrates intermingling of the roots of *P. major* ssp. *major* and *P. lanceolata* was found (see Photo 7.2.1.). Increasing compaction reduced the length of the root systems of all species. The differences in root-system length between the loose and the strongly compacted soils were the largest for *P. lanceolata*. The root systems of *P. major* and *P. media* in the moderately compacted soils were relatively short.

Comparison between the untrampled and trampled series within each plots shows that trampling also reduced the root systems of all species. It is remarkable that even a light trampling regime on the loose soils caused a pronounced reduction in the size of the root systems of *P. media* and *P. lanceolata* (measurement of the surfaces of the root systems as drawn in Fig. 7.2.1., NC and LT, demonstrated a reduction of 48% in LT for *P. media* and 37% for *P. lanceolata*). A smaller reduction was found for *P. coronopus* (13%) and *P. major* (9%). Compared with the untrampled, strongly compacted soils, a heavy trampling regime caused the strongest reduction in the size of the root systems of *P. media* (70%), followed by *P. major* (56%). The reduction was smaller for *P. lanceolata* (35%) and *P. coronopus* (31%). The combined effects of trampling and compaction on root elongation can be seen by comparing the rooting patterns in the untrampled loose soils and those in the heavily trampled plots with the strongly compacted soil. Large effects of trampling with compaction on the root size were found for *P. media* (reduction 87%), *P. major* (80%), and *P. lanceolata* (70%) and relatively small effects were observed for *P. coronopus* (41%).

Root biomass

The distribution of the biomass of the roots within three successive soil layers is given in Fig. 7.2.2. As could be expected, the largest biomass values were found in the upper 12.5 cm of the soil, but there were considerable differences between the species and between the treatments. For all species increasing compaction of the soil was associated with a decrease in biomass in the lower soil layers.

With a light trampling regime, the biomass of the roots of *P. lanceolata* decreased strongly in each soil layer (Fig. 7.2.2., see NC and LT). The other species did not show any important effect of light trampling on the biomass distribution in the soil. Compared with the untrampled, strongly
compacted series, a heavy trampling regime caused a reduction in the biomass of the roots of all species; in each soil layer the reduction was greatest for *P. lanceolata*, followed by *P. media* (Fig. 7.2.2., see SC and HT).

To give an impression of the functioning of the root systems of the four *Plantago* species at the various degrees of compaction and trampling, the shoot-root ratios are presented in Table 7.2.1. A light trampling regime caused an increase in the shoot-root ratio of *P. lanceolata* and *P. major* (see NC and LT). For *P. lanceolata* this increase was due mainly to the considerable decrease in total root biomass (72%); the reduction in shoot biomass of *P. lanceolata* was smaller (60%). Light trampling led to a relatively small reduction in the root biomass of *P. major* (23%), but the shoot biomass increased by 35%. A heavy trampling regime considerably increase the shoot-root ratio of *P. major* and less so that of *P. coronopus* (Table 7.2.1., see SC and HT). Due to heavy trampling a decrease in root biomass (43%) but an increase in shoot biomass (24%) was observed for *P. major*. Compared with the untrampled, strongly compacted soil, a heavy trampling regime caused a higher reduction in biomass of the roots of *P. coronopus* (36%) than in the biomass of the shoots (7%). The data in Table 7.2.1. suggest that in the heavily trampled series the root systems of *P. major* and *P. coronopus* were relatively more efficient: a higher shoot biomass being sustained by a lower root biomass.

Table 7.2.1. Shoot-root ratio of four *Plantago* species at various degrees of soil compaction and trampling

<table>
<thead>
<tr>
<th></th>
<th>NC</th>
<th>LT</th>
<th>SC</th>
<th>HT</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. lanceolata</em></td>
<td>0.5</td>
<td>0.7</td>
<td>0.7</td>
<td>0.7</td>
</tr>
<tr>
<td><em>P. coronopus</em></td>
<td>0.7</td>
<td>0.7</td>
<td>0.5</td>
<td>0.8</td>
</tr>
<tr>
<td><em>P. major ssp. major</em></td>
<td>0.4</td>
<td>0.7</td>
<td>0.4</td>
<td>1.0</td>
</tr>
<tr>
<td><em>P. media</em></td>
<td>0.4</td>
<td>0.4</td>
<td>0.4</td>
<td>0.5</td>
</tr>
</tbody>
</table>

NC = loose soil  
LT = lightly trampled  
SC = strongly compacted soil  
HT = heavily trampled

Seed production

The mean numbers of spikes produced per plant in the various plots are given in Fig. 7.2.3. For *P. coronopus* and *P. major* plants, the numbers of spikes produced in the trampled series are significantly higher than those in the equivalent untrampled series. A high number of spikes was also found for *P. lanceolata* in the lightly trampled series. For both *P. lanceolata* and *P. coronopus*, increasing compaction (Fig. 7.2.3., see L, M, and S of the untrampled series) as well as increasing trampling (Fig. 7.2.3., L, M, and S of the trampled series) caused a considerable decrease in the numbers of spikes. The effects of trampling on the numbers of spikes of *P. lanceolata*
Fig. 7.2.1. Rooting patterns of four *Plantago* species at various degrees of soil compaction and trampling regimes. The contours of the root systems were obtained by measuring of the width of the systems at different depths. For each soil layer the mean width and S.E. (distance between dots) are given.
(Fig. 7.2.1. continued)

NC = loose soil  LT = lightly trampled
MC = moderately compacted soil  MT = moderately trampled
SC = strongly compacted soil  HT = heavily trampled
Photo 7.2.1a. Root systems of four *Plantago* species growing in the loose (NC), moderately compacted (MC), and strongly compacted soils (SC) of the experimental plots. In each photograph the order of the species from the left to the right is *P. major, P. media, P. coronopus, P. major, P. lanceolata* and *P. media.*
Photo 7.2.1b. Root systems of four Plantago species growing in the lightly (LT), moderately (MT), and heavily trampled plots (HT). In each photograph the order of the species from the left to the right is *P. major*, *P. media*, *P. coronopus*, *P. major*, *P. lanceolata*, and *P. media*. 
Fig. 7.2.2. Mean values of the root biomass in three successive soil layers (vertical bars indicate $2 \times$ S.E.)

- **NC** = loose soil
- **MC** = moderately compacted soil
- **SC** = strongly compacted soil
- **LT** = lightly trampled
- **MT** = moderately trampled
- **HT** = heavily trampled
Fig. 7.2.3. Mean numbers of spikes per plant produced at various degrees of soil compaction and trampling (vertical bars indicate $2 \times$ S.E.)

... seem to be more pronounced than the effects of compaction alone. At increasing trampling no negative effects in the numbers of spikes of *P. major* were observed; the most spikes per plant were found on the moderately trampled plots. *P. media* produced few spikes in all treatments. The mean numbers of seeds produced per species in the various plots are given in Fig. 7.2.4. With the exception of *P. major* plants on the loose soils, the mean numbers of produced seeds of all species were significantly lower in all trampled plots than in the equivalent untrampled plots. The decrease in seed production of *P. lanceolata* and *P. coronopus* was greatest between the plants growing on the loose and on the moderately or strongly compacted soils and between the plants of the lightly and the moderately or heavily trampled plots.

The reverse results which were obtained for the numbers of spikes and the numbers of seeds produced by the species in the various treatments show that, in general, considerably fewer seeds were produced per spike in the trampled than in the untrampled plots. These differences are ascribable to the fact that the spikes of the untrampled plants became longer than those of the trampled ones (Table 7.2.2.).
Fig. 7.2.4. Mean numbers of seeds per plant produced at various degrees of soil compaction and trampling (vertical bars indicate $2 \times$ S.E.)

The various treatments also led to differences in the weight of the seeds (Table 7.2.3). The seeds of *P. lanceolata* proved to be lighter in the moderately and heavily trampled plots than in the untrampled plots with the moderately and strongly compacted soils. The reverse was found for seeds of *P. major* and, in the heavily trampled series, for *P. media* seeds. The seeds of *P. coronopus* were heavier in the lightly trampled than in the untrampled plots with the loose soil.

Table 7.2.2. Length of the spikes of four *Plantago* species at various degrees of soil compaction and trampling (mean values in mm ± S.E.)

<table>
<thead>
<tr>
<th></th>
<th>NC</th>
<th>LT</th>
<th>MC</th>
<th>MT</th>
<th>SC</th>
<th>HT</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. lanceolata</em></td>
<td>34.2±2.3</td>
<td>17.5±0.9</td>
<td>22.3±2.3</td>
<td>19.8±2.1</td>
<td>28.7±1.8</td>
<td>17.2±1.4</td>
</tr>
<tr>
<td><em>P. coronopus</em></td>
<td>53.0±4.6</td>
<td>34.0±1.4</td>
<td>28.1±1.1</td>
<td>13.0±1.0</td>
<td>36.9±1.4</td>
<td>17.6±1.0</td>
</tr>
<tr>
<td><em>P. major</em> ssp. <em>major</em></td>
<td>41.2±9.5</td>
<td>33.9±4.6</td>
<td>47.1±8.8</td>
<td>24.4±0.5</td>
<td>44.5±7.0</td>
<td>28.0±1.1</td>
</tr>
<tr>
<td><em>P. media</em></td>
<td>-</td>
<td>-</td>
<td>47.0±1.0</td>
<td>22.0</td>
<td>-</td>
<td>75.0±8.0</td>
</tr>
</tbody>
</table>
TABLE 7.2.3. Mean weight (g) of 1,000 seeds produced by four Plantago species at various degrees of soil compaction and trampling

<table>
<thead>
<tr>
<th></th>
<th>NC</th>
<th>LT</th>
<th>MC</th>
<th>MT</th>
<th>SC</th>
<th>HT</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. lanceolata</em></td>
<td>1.12</td>
<td>1.20</td>
<td>1.21</td>
<td>0.87</td>
<td>1.27</td>
<td>0.83</td>
</tr>
<tr>
<td><em>P. coronopus</em></td>
<td>0.10</td>
<td>0.14</td>
<td>0.15</td>
<td>0.16</td>
<td>0.16</td>
<td>0.14</td>
</tr>
<tr>
<td><em>P. major ssp. major</em></td>
<td>0.18</td>
<td>0.19</td>
<td>0.10</td>
<td>0.26</td>
<td>0.14</td>
<td>0.27</td>
</tr>
<tr>
<td><em>P. media</em></td>
<td>-</td>
<td>-</td>
<td>0.36</td>
<td>0.35</td>
<td>0.36</td>
<td>0.40</td>
</tr>
</tbody>
</table>

NC = loose soil  LT = lightly trampled
MC = moderately compacted soil  MT = moderately trampled
SC = strongly compacted soil  HT = heavily trampled

Discussion

In the study reported in this paper, the effects of soil compaction alone and of trampling and compaction in combination were investigated on the performance of four Plantago species. This experimental approach was chosen because, in the field, compaction can be the result of trampling or other factors such as rainfall and fluctuations in the groundwater level (e.g. Hegarty and Royle 1978; Blom *et al.* 1979). Increasing compaction led to a decrease in the vertical growth of the root systems of all species under study (Fig. 7.2.1.). Many authors have discussed this phenomenon, especially in the agricultural literature (e.g. Schuurman 1971; Taylor 1974). Mechanical compression of elongating roots results in shorter and wider cells, which is probably an effect of endogenously produced ethylene (Barley 1976). Thick roots in compacted soils were also described by Abdalla *et al.* (1969). Soil compaction may increase the internal resistance to water flow within the roots (White 1975). This author suggested that compaction affects the exchange of material between roots and tops, which could lead to reduced plant growth. The experiments presented in this paper also showed that the root systems of all species were shorter in the trampled than in the untrampled series. This reduced growth is probably due mainly to the increased soil compaction caused by the trampling regimes (see Progress Report 1977). The movement of the soil particles under trampling can cause wounding of the roots, which is especially likely in dry sandy soils. It is well known (e.g. Barley 1976) that after wounding the endogenous production of ethylene increases, which in turn results in broader and shorter roots.

The negative effects of compaction alone and of combined trampling and compaction on root elongation were the largest for *P. media* and the smallest for *P. coronopus* (Fig. 7.2.1.).

The drawings of the rooting patterns of *P. major* and *P. coronopus* agree reasonably well with the values for the biomass distribution over the three successive soil layers (See Figs. 7.2.1 and 7.2.2.). Between the three layers in the loose soil, there were only small differences in the width of the root.
system of *P. lanceolata*, but a increasing depth there was a sharp drop in the biomass of the roots of this species, which means that the root density in the upper soil layers was much higher than in the lower ones. Increasing soil compaction caused by the light trampling regimes on the loose soils, also resulted in a relatively high root density for *P. media* (see Figs. 7.2.1. and 7.2.2.). Changes in root density may affect the plant’s ability to compete for nutrients (Andrews & Newman 1970). Mineral analyses of shoot and root material of the plants grown in the various plots will be made in the near future to obtain an impression of the effects of competition caused by different root densities and, especially in case of *P. major* and *P. lanceolata*, the intermingling of root systems. Compared with the untrampled series, light and heavy trampling caused an increase in the shoot-root ratio of *P. major* (Table 7.2.1.), due mainly to the increase in the shoot biomass under trampled conditions. This surprising reaction of *P. major* is probably to be ascribed to the occurrence of root competition in this experiment. As can be seen in Photos 7.2.1a.,b., and Fig. 7.2.1., the large root systems of the *P. lanceolata* plants growing in the loose soils penetrated strongly into the soil volume reserved for *P. major*. This suggests that *P. lanceolata* may negatively affect the growth of *P. major*. In the trampled plots the interference between the roots of these two species appeared to be much smaller. Under the conditions of this experiment the enhanced root efficiency of *P. major* in trampled soils may be ascribed, on the one hand, to the absence of competition and, on the other, to the better water supply in compacted soils. In a recent paper Newberry and Newman (1978) reported on the effects of root competition between *P. lanceolata* and some other species. These authors concluded, however, that root competition on a nutrient-poor soil may promote the coexistence between species. Compared with the untrampled series, trampling had a positive effect on the number of spikes of *P. coronopus* and *P. major* (Fig. 7.2.3.). In the case of *P. lanceolata*, light trampling resulted in more spikes. Increasing compaction as well as increasing trampling reduced the numbers of spikes of both *P lanceolata* and *P. coronopus*. Another effect of trampling was a reduction in the length of the spikes of all species (Table 7.2.2.), which influenced seed production. The strong reduction of spike length in *P. lanceolata*, even under the light trampling regime, was remarkable. For this species and for *P. media*, mechanical damage under a heavy trampling regime meant that no seeds were produced in the upper parts of the spikes. The effects of the various degrees of compaction and of the different trampling regimes on the numbers of spikes were the largest for *P. lanceolata* and *P. coronopus* and the smallest for *P. major* and *P. media*, as previously found for the diameters of the rosettes (Blom 1978b).

Trampling and compaction also influenced the weights of the seeds of the *Plantago* species (Table 7.2.3.). Seeds of *P. lanceolata* were lighter at increasing trampling intensity, whereas the weight of the seeds of *P. major*
and *P. media* increased under these conditions. Only slight effects of trampling on the weight of *P. coronopus* seeds were observed, but increasing compaction caused an increase in the seed weight of this species. Changes in seed weight due to different environmental conditions were observed for other species by Salisbury (1974). To understand the meaning of these observations, research on the seed distribution and the germination capacity in relation to seed weight under field conditions will be necessary. Preliminary tests indicated that the germination capacity of seeds from trampled *P. lanceolata* and *P. media* plants was lower than that of the untrampled individuals.

In conclusion, it can be stated that the root development of the species under study was strongly affected by the effects of soil compaction. The additional effects of trampling on the root systems were probably caused mainly by the increasing compaction of the trampled soils. The shoot-root ratios (Table 7.2.1.) suggest that *P. major* ssp. *major* and *P. coronopus* plants have root systems which are more effective under trampled conditions than in the absence of trampling. Negative effects of soil compaction on seed production were clearly demonstrated. This reduction in seed production must be ascribed to the reduced vitality of the plants in compacted soils. A direct effect of trampling on the seed production of *P. lanceolata*, *P. coronopus*, and *P. major* was observed. For reasons unknown, *P. media* flowered very poorly on the loose and moderately compacted soils, and therefore, for the time being, no meaning can be assigned to the relatively high seed production of this species in the strongly compacted and heavily trampled soils.

References


Blom, C.W.P.M. – Germination, seedling emergence and establishment of