6.2. THE INFLUENCE OF TRAMPLING AND SOIL COMPACTNESS ON SEEDLING DISTRIBUTION OF SOME PLANTAGO SPECIES SOWN ON PLOTS IN THE DUNE AREA OF VOORNE (C. W. P. M. Blom)

6.2.1. Introduction

The research on the influence of trampling and soil compactness on the distribution of some Plantago species was continued in sowing experiments on plots in the dune area of Voorne. Preceding experiments (Blom, Progress Report 1973) concerned the influence of trampling and soil compactness under optimal and low moisture levels on the germination of seeds of Plantago lanceolata, P. coronopus, P. major, and P. media in barren dune soils. In the experiments under discussion here the seeds were sown on natural dune soils with a cover of other plant species. The aim of these sowing experiments is to get an impression of the influence of trampling, soil compactness, soil humidity, and competition effects of the surrounding vegetation on the emergence and establishment of Plantago seedlings.

6.2.2. Material and methods

Fourteen plots were chosen in the dune area of Voorne, six of them in the middle of paths, five plots on edges of paths, and three on sites rarely trodden by men. Some characteristics of the plots are given in Table 8. Besides trampling and soil compactness, other factors including the soil humidity and the height and coverage of the vegetation layer are important for the emergence and development of seedlings. The vegetation on paths in the dunes is mostly low, and the soil surface is not entirely covered by plants. The herb layer is higher on the edges of the paths than on them, and the entire surface is covered by vegetation.

On sites with loose soil, rabbits keep the vegetation layer open and mostly very low. The soil humidity depends on the ground water level, the physical and chemical composition of the soil, and the total biomass of the vegetation. In choosing the plots an attempt was made to obtain some diversity in soil moisture contents.

In the beginning of April, 1974, the plots (30 × 30 cm) were sown with a mixture of Plantago lanceolata, P. coronopus, P. major, and P. media (200 seeds of each species) distributed uniformly over the plots. Every fortnight the location of the individual plants were recorded on a map (scale 1:1), and the study was interrupted at the end of the growth season. For comparison, control plots close to the sown plots were studied to get an impression of the spontaneous appearance of the Plantago species.

6.2.3. Results

The results of these experiments are shown in Tables 9a, 9b, and 9c as the number of living Plantago plants and the percentages of plants
which died off during the research period. The percentages of succumbed plants were determined in relation to the total numbers of emerged seedlings. Seeds of *P. lanceolata* and *P. coronopus* are able to germinate on untrodden sites with a loose, dry soil (Table 9a). The data in Table 9b show that on occasionally trodden sites with a moderately compacted soil, *P. lanceolata* and *P. coronopus* also occurred more frequently than the other *Plantago* species but had a higher mortality than on loose dune soils. Table 9c shows that all four species, but particularly *P. major* and *P. media*, occur more often on compacted and trodden sites than on loose or moderately compacted soils.

During the research period *P. coronopus* showed the highest mortality of all the *Plantago* species; the lowest percentages of dead plants were found for *P. major* and *P. lanceolata*.

### 6.2.4. Discussion

In field situations the emergence and development of seedlings are dependent on the effects of a complex of unknown factors, including the quantity of *Plantago* seeds already present in the plots at the start of the research period, the quantity of seeds immigrating into a plot, and the quantity of seeds that disappear from a plot during this period.

Some control plots were investigated to get an impression of the seedlings naturally present on a site, for comparison with a sown plot. According to the findings in the unseeded plots, *P. lanceolata* had been present in the vicinity of all of the experimental plots, *P. coronopus* occurred in the direct surroundings of plots M₂, M₃, V₂, V₃, and *P. major* grew sparsely near plots V₄, V₅, and V₆.

As already mentioned, the combined effect of trampling, soil compaction,

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<th>Number</th>
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<th>Soil humidity</th>
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<td>O₁</td>
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<td>dune grassland</td>
<td>dry</td>
</tr>
<tr>
<td>O₂</td>
<td>scarcely trodden, not compacted</td>
<td>dune grassland</td>
<td>dry</td>
</tr>
<tr>
<td>O₃</td>
<td>scarcely trodden, not compacted, barren soil</td>
<td>dune grassland</td>
<td>dry</td>
</tr>
<tr>
<td>M₁</td>
<td>edge, sometimes trodden, moderately compacted</td>
<td>dune grassland</td>
<td>dry</td>
</tr>
<tr>
<td>M₂</td>
<td>edge, sometimes trodden, moderately compacted</td>
<td>dune grassland</td>
<td>moderately humid</td>
</tr>
<tr>
<td>M₃</td>
<td>edge, sometimes trodden, moderately compacted</td>
<td>dune grassland</td>
<td>humid</td>
</tr>
<tr>
<td>M₄</td>
<td>edge, sometimes trodden, moderately compacted</td>
<td>dune slack</td>
<td>wet</td>
</tr>
<tr>
<td>M₅</td>
<td>edge, sometimes trodden, moderately compacted</td>
<td>dune slack</td>
<td>humid</td>
</tr>
<tr>
<td>V₁</td>
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<td>dune grassland</td>
<td>dry</td>
</tr>
<tr>
<td>V₂</td>
<td>path, trodden, compacted soil</td>
<td>dune grassland</td>
<td>humid</td>
</tr>
<tr>
<td>V₃</td>
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<td>humid</td>
</tr>
<tr>
<td>V₄</td>
<td>path, frequently trodden, compacted soil</td>
<td>dune slack</td>
<td>humid</td>
</tr>
<tr>
<td>V₅</td>
<td>path, frequently trodden, compacted soil</td>
<td>dune slack</td>
<td>humid</td>
</tr>
<tr>
<td>V₆</td>
<td>path, frequently trodden, compacted soil</td>
<td>dune slack</td>
<td>wet</td>
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</table>
Provisional Report 1974

Table 9a. Numbers of living (+) and percentages of dead (− %) Plantago plants on the non-compacted sown plots.

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<th>O3</th>
<th>15/3 O1</th>
<th>O2</th>
<th>O3</th>
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<th>O2</th>
<th>O3</th>
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<td>3</td>
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<td>1</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>− %</strong></td>
<td></td>
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<td>5</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. coronopus</em></td>
<td><strong>+</strong></td>
<td></td>
<td>7</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>− %</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. major</em></td>
<td><strong>+</strong></td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. media</em></td>
<td><strong>+</strong></td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>− %</strong></td>
<td></td>
<td></td>
<td></td>
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<th>O2</th>
<th>O3</th>
<th>26/6 O1</th>
<th>O2</th>
<th>O3</th>
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<th>O2</th>
<th>O3</th>
</tr>
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<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>− %</strong></td>
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<td>13</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. coronopus</em></td>
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<td></td>
<td>10</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>− %</strong></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. major</em></td>
<td><strong>+</strong></td>
<td></td>
<td>100</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>− %</strong></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. media</em></td>
<td><strong>+</strong></td>
<td></td>
<td>100</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>− %</strong></td>
<td></td>
<td></td>
<td></td>
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<th>O3</th>
<th>15/10 O1</th>
<th>O2</th>
<th>O3</th>
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<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td><strong>− %</strong></td>
<td></td>
<td>27</td>
<td>24</td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
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<td><em>P. coronopus</em></td>
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<td></td>
<td>23</td>
<td>7</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>− %</strong></td>
<td></td>
<td>20</td>
<td>9</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. major</em></td>
<td><strong>+</strong></td>
<td></td>
<td>4</td>
<td>5</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>− %</strong></td>
<td></td>
<td>20</td>
<td>100</td>
<td>16</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. media</em></td>
<td><strong>+</strong></td>
<td></td>
<td>4</td>
<td>5</td>
<td>5</td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
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<td></td>
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</tr>
</tbody>
</table>

Soil moisture level, and competition of surrounding plants is important for the presence or absence of a plant species. Table 10 shows the data on some of these factors, together with the total percentages of new Plantago plants. In comparison with the other Plantago species, *P. lanceolata* is most tolerant to the factors indicated in Table 10. *P. coronopus* seems to occur in smaller numbers, mainly on partially covered sites, and on open dry dune sand soils more frequently than on humid, incom-
Table 9b. Numbers of living (+) and percentages of dead (− %) Plantago plants on the moderately compacted sown plots.

<table>
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<td>M₃</td>
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<td>3</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>− %</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>coronopus</td>
<td>+</td>
<td>—</td>
<td>—</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>− %</td>
<td>—</td>
<td>—</td>
<td>—</td>
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<tr>
<td>major</td>
<td>+</td>
<td>—</td>
<td>—</td>
<td>1</td>
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<td></td>
<td>− %</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>media</td>
<td>+</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>− %</td>
<td>—</td>
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<td>M₃</td>
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<td>50</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
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<td>—</td>
<td>—</td>
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</tr>
<tr>
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</tr>
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</tr>
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</tr>
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<td>—</td>
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Table 9c. Numbers of living (+) and percentages of dead (−%) *Plantago* plants on the compacted sown plots.

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<td>82</td>
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<td>V2</td>
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<th>9/7</th>
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<td>60</td>
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<td>3</td>
<td>1</td>
</tr>
<tr>
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<td>Plot no.</td>
<td>Vi</td>
<td>V2</td>
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<td>16</td>
</tr>
<tr>
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<td>30</td>
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<tr>
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</tr>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Date</th>
<th>22/8</th>
<th>5/9</th>
<th>15/10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Plot no.</td>
<td>Vi</td>
<td>V2</td>
</tr>
<tr>
<td><em>P. lanceolata</em></td>
<td></td>
<td>14</td>
<td>16</td>
</tr>
<tr>
<td>coronopus</td>
<td></td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>major</td>
<td></td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>media</td>
<td></td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>
Table 10. Some environmental factors related to the emergence of *Plantago* seedlings

<table>
<thead>
<tr>
<th>Plot nr.</th>
<th>Mean height vegetation (cm)</th>
<th>Mean penetr. values</th>
<th>Soil humidity (% dry weight)</th>
<th>Emerged plants (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cover (%)</td>
<td>Trampling intensity</td>
<td>lowest values</td>
<td>highest values</td>
</tr>
<tr>
<td>O₁</td>
<td>0</td>
<td>0.1</td>
<td>1.1</td>
<td>6.5</td>
</tr>
<tr>
<td>O₂</td>
<td>5</td>
<td>0.2</td>
<td>2.0</td>
<td>7.5</td>
</tr>
<tr>
<td>O₃</td>
<td>0</td>
<td>0.1</td>
<td>3.0</td>
<td>16.1</td>
</tr>
<tr>
<td>M₁</td>
<td>15</td>
<td>100</td>
<td>4.4</td>
<td>39.4</td>
</tr>
<tr>
<td>M₂</td>
<td>15</td>
<td>90</td>
<td>11.6</td>
<td>46.4</td>
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<td>M₃</td>
<td>10</td>
<td>100</td>
<td>42.8</td>
<td>104.2</td>
</tr>
<tr>
<td>M₄</td>
<td>10</td>
<td>100</td>
<td>50.8</td>
<td>136.8</td>
</tr>
<tr>
<td>M₅</td>
<td>10</td>
<td>100</td>
<td>34.6</td>
<td>95.5</td>
</tr>
<tr>
<td>V₁</td>
<td>7</td>
<td>85</td>
<td>+</td>
<td>0.1</td>
</tr>
<tr>
<td>V₂</td>
<td>5</td>
<td>70</td>
<td>++</td>
<td>20.5</td>
</tr>
<tr>
<td>V₃</td>
<td>5</td>
<td>70</td>
<td>++</td>
<td>11.9</td>
</tr>
<tr>
<td>V₄</td>
<td>2</td>
<td>40</td>
<td>+++</td>
<td>20.5</td>
</tr>
<tr>
<td>V₅</td>
<td>3</td>
<td>50</td>
<td>+++</td>
<td>23.2</td>
</tr>
<tr>
<td>V₆</td>
<td>3</td>
<td>40</td>
<td>+++</td>
<td>45.3</td>
</tr>
</tbody>
</table>

* Symbols: trampling: — absent; ± sometimes; + moderate; ++ rather frequent; +++ very frequent.

** penetrometer values: at a depth of 5 cm (penetrometer units).

pletely covered sites. There are more *P. major* plants on trodden, compacted, humid, and open sites; and the same holds for *P. media*.

For all of the species studied, high percentages of seedlings occurred on the paths, probably because trampling led to increased contact between the seed surface and the soil, which in turn results in an increase in the rate of water uptake. In the absence of trampling, germination of seeds landing on compacted surfaces may be reduced, because of the disappearance of microrelief during the course of the compaction process (Sheldon, 1974). This effect is more important for large seeds like those of *P. lanceolata* than for small seeds like those of *P. coronopus* (Harper et al., 1965). As compared with the other sites on the paths, plot V₁ had a small number of plants of *P. coronopus, P. major,* and *P. media.* This was probably due to the higher density of the surrounding vegetation. As compared with the other plots on the paths, plot V₆ showed relatively few seedlings of all the species under study, probably because of the wetness of the soil. Table 9 shows that increased trampling causes an increase in the number of dead seedlings. Under these same conditions fewer *P. lanceolata* plants succumbed than would be expected from the results of earlier greenhouse experiments (Blom, Progress Report 1973).
This discrepancy is explained by the fact that the trampling intensity in the field is less regular than the simulated trampling applied in the greenhouse. It is remarkable that relatively few individuals of *P. coronopus* were present, indicating that the presence of the typical dune species depends on unknown factors. There is some evidence that the distribution of *P. coronopus* is related to the presence of shells and mosses. *P. media* was found in the lowest numbers, possibly because this species does not occur naturally in the dunes. At the end of the research period the number of *P. major* plants decreased, probably due to shoot mortality during the winter. Studies on the emergence of *Plantago* seeds in the dune area will be continued.

References


6.3. A NODULATION STUDY ON HIPPOPHAE RHAMNOIDES L. (P. A. I. Oremus)

6.3.1. Introduction

A preliminary field survey on *Hippophaë rhamnoides* has shown that the total number of nodules on suckers of the same age varies greatly from site to site. The experiment described here represents a first attempt to find out whether these differences can be explained by differences in the number of infective particles (the infectious state of the root-nodule endophyte) in the soil. For this purpose, the nodulation of plants grown in soil samples from different habitats was compared with that of plants grown in the same samples to which infective particles had been added.

6.3.2. Material and methods

Sample sites

a. sandy beach, *H. rhamnoides* absent,

b. outer dunes with *Ammophila arenaria* vegetation, *H. rhamnoides* absent,

c. inner dunes with *H. rhamnoides* vegetation, in places where young suckers were not nodulated, and

d. inner dunes with *H. rhamnoides* vegetation, in places where young suckers were abundantly nodulated.

Plant material

Sterilized seeds of *H. rhamnoides* (for techniques, see Oremus, 1971)