OCCURRENCE OF THREE PLANTAGO SPECIES IN COASTAL DUNE GRASSLANDS IN RELATION TO PORE-VOLUME AND ORGANIC MATTER CONTENT OF THE SOIL

R. NOË AND C. W. P. M. BLOM

Institute for Ecological Research, Department of Dune Research 'Weevers' Duin', Duinzoom 20a, 3233 EG Oostvoorne, The Netherlands

SUMMARY

(1) The relationships between the distribution of three Plantago species and some soil characteristics were investigated.

(2) The total pore-volume of the soil appeared to be significantly lower in plots with Plantago lanceolata than in plots without this species. Plantago major was found in relatively wet sites with a low percentage of air-filled volume and relatively high organic matter content. Plantago coronopus was observed in soils with a relatively low total pore-volume.

(3) There are indications that two types of P. lanceolata occurred in the study area; one type, of large individuals, on wet sites and the other, of small individuals, on drier parts of the area.

INTRODUCTION

Trampling and the resulting compaction of the soil are important factors for the distribution of P. major L. ssp. major, and to a lesser degree, P. coronopus L. (e.g. Westhoff 1967; Oberdorfer 1970; Liddle & Greig-Smith 1975b; Blom, Husson & Westhoff 1979). Plantago lanceolata can be found in lightly trampled meadows and untrampled hayfields (e.g. Sagar & Harper 1960; Oberdorfer 1970; Blom, Husson & Westhoff 1979).

Susceptibility to trampling and soil compaction strongly depends on the stage in the life-cycle of the plants (Blom 1976, 1977). In a sandy soil, compaction influences plant growth through high mechanical resistance, a reduction in soil air and soil water porosity, but due to greater capillarity a higher moisture content exists in the upper layers of the soil (Rosenberg 1964; Warkentin 1971; Grable 1971).

In the field two methods are commonly used to record the effect of environmental factors on the distribution of plant species. The first one is based on sampling of transects in which a gradient is supposed to be present and the second on selection of plots in different zones (e.g. Goldsmith, Munton & Warren 1970; Burden & Randerson 1972; Liddle & Greig-Smith 1975a, b).

In the study area, evident gradients in trampling intensity are present only around cattle tracks and drinking ponds. The larger part of the area is relatively lightly trampled and the distribution pattern of P. lanceolata, an abundant species, is not obvious. Neither of the methods mentioned above are appropriate for the study of the distribution of this species and an alternative sampling method was used.

In this study an attempt was made to answer two questions: are there differences in pore-volume and organic matter content of the soil on sites with and without P. lanceolata,
and what is the relationship between the biomass per unit area of that species and the values of the soil parameters?

The results for *P. lanceolata* were compared with those for *P. major* and *P. coronopus*.

**METHODS**

*The study area*

The old dune-grassland ‘Westduinen’ (Goeree, the Netherlands) has been in use as common grazing for some centuries. In recent years about thirty cows and twenty-five horses have grazed, except in the winter, on an area of 176 ha. Organic matter accumulation reaches a maximum in slacks, and carbonates have been leached completely from the upper 30 cm or more. The organic matter content generally varies from 2 to 20% in the 0–10 cm layer (Troelstra 1978). A detailed description of the vegetation is given by Blom, Husson & Westhoff (1979).

**Sampling**

*Series A*

An area of c. 19 ha was chosen for this study; c. one-third is quite flat, the remaining part undulating. In September 1977, ten transects, each consisting of ten plots, were sampled. Randomly selected intersections of a 50-m grid were the starting-points of the transects, which were located in a randomly selected compass-direction. Each 5th metre of the transect was used as an angular point of a plot of 0.5 x 0.5 m. The biomass of *P. lanceolata* was recorded in each plot.

For each plot the following soil characteristics were determined.

(a) The air-filled volume (% by volume), measured using a vacuum pycnometer, as the mean of three samples of 100 cm³ each, taken at a depth of 2–6 cm.

(b) The water-filled volume (% by volume) determined by weighing the same samples before and after drying at 105 °C for 24 h.

(c) The total pore-volume calculated as the sum of the air-filled and the water-filled volumes.

(d) The organic matter content (% dry weight of soil; loss-on-ignition, 410 °C with correction for moisture content) determined in a mixed sample of four cores of the upper 5 cm layer, dried and sieved at 1 mm.

*Series B and C*

Twenty plots were randomly chosen within zones where *P. major* was the most common *Plantago* species (Series B). The Series C studies were made 6 months earlier on forty-nine plots, randomly selected, in an area where *P. coronopus* was more common. Biomass and soil data were collected.

*Estimation of biomass*

The dry weights of non-flowering plants, or plants with only short spikes, were estimated by multiplying the number of green leaves (*L*) by the largest diameter of the rosette (*D*). In the case of more than one rosette per plant the value *L* x *D* was calculated per rosette and the values were added. In a separate experiment the correlation between dry weight and (*L* x *D*) was found to be 0.89 for *P. lanceolata* (eighty-four specimens) and 0.92 for *P. coronopus* (eighty-two specimens).

The relative biomass per plot was estimated by adding all values of *L* x *D*. 
RESULTS

The independence of the plots in each transect of Series A was tested by calculating the serial correlation coefficient with the values of organic matter content and total pore-volume as parameters (Table 1).

*Plantago lanceolata* did not occur in sixty-one of the 100 plots of Series A (Group AO). In eight of the plots in which the species was present, only one individual per plot was found, while only three plots had more than forty rosettes, the highest number being 193 (Group AL: plots with *P. lanceolata*). The mean values of the soil parameters are given for the groups AO and AL and the differences between the groups have been tested with the Mann–Whitney-U-test (Table 2).

In Series B, *P. major* was found in eighteen of the twenty plots (Group BM) and *P. lanceolata* in fourteen plots (Group BL). In Series C *P. coronopus* was present in all plots.

Total pore-volume and organic matter content can be compared between the three series (Fig. 1). The differences in organic matter content and total pore-volume between Series A and B indicate, that the marked difference between the air/water ratios is real. The values for organic matter content found in Series C plots resemble those found in Series A. The total pore-volume, however, is significantly smaller in Series C than in Series A.

Plotting the relative biomass per plot against each of the four soil-characteristics showed in all cases clusters of points without a clear structure. Simple regressions have been calculated (Table 3).

**Table 1.** A calculation of the serial correlation coefficient (r) with the values of organic matter content and total pore-volume of the plots in ten transects of Series A. The correlation between plots in a transect is significantly positive when \( r > 0.36 \) \((n = 10; \alpha = 0.05; \text{one-tailed test})\)

<table>
<thead>
<tr>
<th>Transect of series A</th>
<th>Organic matter content</th>
<th>Total pore-volume</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.35</td>
<td>0.04</td>
</tr>
<tr>
<td>2</td>
<td>0.25</td>
<td>0.31</td>
</tr>
<tr>
<td>3</td>
<td>0.20</td>
<td>0.00</td>
</tr>
<tr>
<td>4</td>
<td>-0.26</td>
<td>0.16</td>
</tr>
<tr>
<td>5</td>
<td>-0.14</td>
<td>0.19</td>
</tr>
<tr>
<td>6</td>
<td>-0.09</td>
<td>0.19</td>
</tr>
<tr>
<td>7</td>
<td>-0.30</td>
<td>0.29</td>
</tr>
<tr>
<td>8</td>
<td>-0.51</td>
<td>-0.88</td>
</tr>
<tr>
<td>9</td>
<td>-0.04</td>
<td>-0.59</td>
</tr>
<tr>
<td>10</td>
<td>-0.41</td>
<td>-0.59</td>
</tr>
</tbody>
</table>

**Table 2.** Mean values with, in parentheses, 95% confidence limits of soil characteristics in a Series of 100 plots randomly chosen (Series A)

<table>
<thead>
<tr>
<th></th>
<th><em>P. lanceolata</em> present (AL)</th>
<th><em>P. lanceolata</em> absent (AO)</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air-filled pore-volume</td>
<td>49.7 (48.5–50.9)</td>
<td>51.9 (51.0–52.8)</td>
<td>0.0128*</td>
</tr>
<tr>
<td>(% by volume)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water-filled pore-volume</td>
<td>8.4 (7.5–9.3)</td>
<td>8.5 (7.8–9.2)</td>
<td>0.7566</td>
</tr>
<tr>
<td>(% by volume)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total pore-volume</td>
<td>58.2 (57.1–59.3)</td>
<td>60.4 (59.3–61.5)</td>
<td>0.0138*</td>
</tr>
<tr>
<td>(% by volume)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Organic matter content</td>
<td>7.2 (6.5–7.9)</td>
<td>8.3 (7.7–8.8)</td>
<td>0.0178*</td>
</tr>
<tr>
<td>(% dry wt of soil)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Significant (Mann–Whitney-U-test) Level of significance: 0.05; two-tailed test.
Number of plots: AO: 61; AL: 39.
Plantago, pore-volume and organic matter

Fig. 1. Some characteristics of the soil in which *P. lanceolata*, *P. major* and *P. coronopus* occur in a coastal grassland ("Westduinen", the Netherlands). (a) Air-filled volume; (b) water-filled volume; (c) total pore volume; (d) organic matter content. AL—Series A; *Plantago lanceolata* present, BL—Series B; *Plantago lanceolata* present, BM—Series B; *Plantago major* present, C—Series C; *Plantago coronopus* present. Mean values with 95% confidence limits are shown.

Table 3. Regression analysis of the relationship between some soil characteristics and estimates of the biomass of *P. lanceolata* and *P. major*

<table>
<thead>
<tr>
<th></th>
<th>Series A</th>
<th></th>
<th>Series B</th>
<th></th>
<th>Series B</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Thirty-nine plots with <em>P. lanceolata</em> present</td>
<td>Fourteen plots with <em>P. lanceolata</em> present</td>
<td>Eighteen plots with <em>P. major</em> present</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass with:</td>
<td>t-value</td>
<td>correlation coefficient</td>
<td>t-value</td>
<td>correlation coefficient</td>
<td>t-value</td>
<td>correlation coefficient</td>
</tr>
<tr>
<td>Organic matter</td>
<td>-0.57</td>
<td>-0.09</td>
<td>2.03</td>
<td>0.51</td>
<td>0.71</td>
<td>0.17</td>
</tr>
<tr>
<td>Air-filled volume</td>
<td>-2.72</td>
<td>-0.41*</td>
<td>2.22</td>
<td>0.64*</td>
<td>-2.61</td>
<td>-0.55*</td>
</tr>
<tr>
<td>Water-filled volume</td>
<td>0.77</td>
<td>0.13</td>
<td>0.98</td>
<td>0.27</td>
<td>2.29</td>
<td>0.50*</td>
</tr>
<tr>
<td>Total pore-volume</td>
<td>-2.21</td>
<td>-0.34*</td>
<td>1.76</td>
<td>0.45</td>
<td>0.48</td>
<td>0.12</td>
</tr>
<tr>
<td>Critical value of t</td>
<td>2.03</td>
<td>2.18</td>
<td>2.12</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Significant at *P* = 0.05.

The plants of *P. lanceolata* found in Series B were generally larger than those found in Series A. The mean rosette-diameter was 6.35 ± 0.12 cm (620 rosettes) in Series A and 11.89 ± 0.47 cm (105 rosettes) in Series B.

DISCUSSION

A number of sampling methods, varying from unrestricted random selection to systematic sampling (e.g. Southwood 1976), can be used to reveal relations between the distribution of...
plant species and certain soil characteristics. The sampling method used in this study (Series A) seems to be useful in areas with a relatively homogeneous vegetation. In selecting plots, fully-independent random positioning would be more desirable, but is more time consuming. The method of Series A was more practicable and approximated well to the required random selection. In areas with evident vegetation patterns, stratified methods, e.g. based on ecological knowledge, are to be preferred. Random sampling (as in Series B) may then be used within limited zones (e.g. Liddle & Greig-Smith 1975a, b).

*Plantago lanceolata* occurred in sites with relatively wide ranges of organic matter content and pore-volumes. The air-filled volume, however, seems to be of significance to the distribution. In Series A the group of plots without *P. lanceolata* had slightly, but significantly more air-filled pore-space. In Series B *P. lanceolata* appeared to occur under wet conditions with low air-filled pore-spaces.

For *P. lanceolata* the correlation between biomass and air-filled volume was negative in Series A. In Series B, in which values of air-filled pore-volume were generally much lower, the correlation with biomass was positive. The distribution of *P. lanceolata* may be limited by a minimum as well as a maximum air-filled pore-volume, but the habitats with values in the middle range, where the optimum with respect to this factor might be expected are missing.

There are two possibilities to explain this phenomenon. Firstly, a study of the pF-curve of a sandy soil shows that at a certain pF-level a slight difference in pF means a great change in water volume (cf. Scheffer & Schachtschabel 1976); therefore values in an intermediate range can hardly be expected. Secondly, high levels of water-filled volume and of organic matter are found mainly in areas which are submerged in winter. On the slopes of these slacks the transition between soils which are relatively high and relatively low in organic matter seems to be rather sharp. This means that the possibility in time as well as in space of finding intermediate values of air-filled pore-volumes will be relatively low.

Individuals of *P. lanceolata* observed on the plots with a low organic matter content and a low total pore-volume (Series A) were identified as var. *sphaerostachya* Mert. and Koch and the other (Series B) as var. *lanceolata*.

*Plantago major* occurred on wet places on soils with a relatively high organic matter content. For seedling establishment and growth *P. major* needs relatively bare soils (Sagar & Harper 1960; Blom 1979). This species has high resistance to environmental stress (trampling, compaction), but low competitive ability (Grime 1979).

*Plantago coronopus* occurred on moderately trampled sites with a relatively low organic matter content and a small total pore-volume.

**ACKNOWLEDGMENTS**

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**REFERENCES**


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