the large differences in structure and density of the vegetations, a quantitative
measure was needed. We chose light transmission for this purpose, i.e., the per-
centage of light penetrating to the soil level in the summer period (May-August
1979).

Comparison of the densities of one population in October of 1978 and 1979 showed
that relatively wide differences in positive or negative population growth occurred.
These differences were correlated with light transmission in the summer and thus
in some way with the density of the vegetation. As can be seen from Fig. 10.1,
the population density increased in open vegetations, but decreased considerably
in the densest vegetations.

Such trends in population growth can of course be caused by trends in either
natality or mortality, or both. There are indications that differences in the occur-
rence of seedlings also contributed to this trend. Secondary rosettes were not
taken into account in the calculations. Further analysis of the data is needed,
however, before more details can be given.

More information is available on survival. No correlation was found between
survival during the winter and the density of the vegetation, but in the summer
period (May-October) survival was correlated with light transmission.

Because survival was also correlated with size, the plants were divided into
three categories: seedlings (with cotyledons), plants with one to three leaves,
and plants with four or more leaves. Fig. 10.2 (upper graphs) shows the survival
from May to October for these categories of plants in relation to the light trans-
mission. Apart from the differences in the general level of survival, a positive
correlation was found for the two groups with the smallest individuals. This points
to an important contribution by survival in the summer to the trend in population
density. Even when survival is calculated for a period of a whole year (May 1978-
May 1979), the correlation is still present.

Light transmission is used here as an indicator for the general structure of the
vegetation. However, most of the mortality occurred in the period during which
the biomass of the vegetation is greatest, e.g., before the hayfields are mown. It
is therefore possible that light had a direct influence on survival, but other fac-
tors that vary simultaneously may have been involved or been more important.
Large plants can compete adequately for light in high vegetations because their
upward-growing leaves reach lengths of 40-60 cm or more.

These findings raise the question of how populations of Plantago lanceolata
maintain themselves in dense vegetations. This is also relevant with respect to
the finding that populations of this species in some situations (e.g., after disturb-
ance) show a dramatic explosion followed by a decrease in numbers (van den
Bergh 1979). To investigate these problems, further demographic studies will be
concentrated on a few selected populations in which more attention will be given
to the spatial distribution of individuals in the population.

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11. Experimental ecology of Plantago maritima (C.W.P.M. Blom and J. van Hees-
wijk)

INTRODUCTION AND METHODS

Some hypotheses originating from the comparison of demographic properties of
Plantago species in relation to their environment are now being tested in exper-
imental studies. In this report an experiment concerning *Plantago maritima*, a species growing on mud flats and beach plains, is described. At Kwade Hoek (island of Goeree, The Netherlands) seeds of *P. maritima* were sown in four series of three plots each. Series A was situated on the edge of the inner dunes, an area influenced considerably by rabbits, series B on an intensively trampled cattle path, and series C and D near creeks. Series C was flooded during each high-tide period, series A, B, and D were flooded only during extremely high tides. On each plot 100 seeds (collected in the preceding year) were sown in a regular pattern. All these areas were natural habitats of *P. maritima*. In the zones of A, B, and C the naturally occurring numbers of *P. maritima* plants were relatively low (0-5 individuals a square metre). In series D higher numbers were observed, and sometimes more rosettes per individual plant were found.

Table 11. Vegetation analysis of the *Plantago maritima* sowing plots at Kwade Hoek, Goeree (The Netherlands). Per species the percentages of soil covering are given

<table>
<thead>
<tr>
<th>Series</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total cover</td>
<td>60%</td>
<td>20%</td>
<td>80%</td>
<td>100%</td>
</tr>
<tr>
<td>Cover of droppings</td>
<td>15%</td>
<td>—</td>
<td>—</td>
<td>5%</td>
</tr>
<tr>
<td>Maximum height of herb layer</td>
<td>5-15 cm</td>
<td>5 cm</td>
<td>5 cm</td>
<td>5 cm</td>
</tr>
<tr>
<td><em>Plantago maritima</em></td>
<td>5-10%</td>
<td>&lt; 5%</td>
<td>—</td>
<td>10%</td>
</tr>
<tr>
<td><em>Plantago coronopus</em></td>
<td>5-10%</td>
<td>—</td>
<td>—</td>
<td>&lt; 5%</td>
</tr>
<tr>
<td><em>Carex arenaria</em></td>
<td>10%</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Honkenya peploides</em></td>
<td>10-15%</td>
<td>&lt; 5%</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Festuca rubra</em></td>
<td>&lt; 5%</td>
<td>—</td>
<td>—</td>
<td>90%</td>
</tr>
<tr>
<td><em>Atriplex hastata</em></td>
<td>5-10%</td>
<td>—</td>
<td>—</td>
<td>&lt; 5%</td>
</tr>
<tr>
<td><em>Spergularia media</em></td>
<td>&lt; 5%</td>
<td>5%</td>
<td>&lt; 5%</td>
<td>—</td>
</tr>
<tr>
<td><em>Poa pratensis</em></td>
<td>10-15%</td>
<td>&lt; 5%</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Elytrichia repens</em></td>
<td>&lt; 5%</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Salicornia europaea</em></td>
<td>—</td>
<td>&lt; 5%</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Puccinellia maritima</em></td>
<td>—</td>
<td>—</td>
<td>40%</td>
<td>—</td>
</tr>
<tr>
<td><em>Glaux maritima</em></td>
<td>—</td>
<td>—</td>
<td>40%</td>
<td>25%</td>
</tr>
<tr>
<td><em>Aster tripolium</em></td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>&lt; 5%</td>
</tr>
</tbody>
</table>

Table 11 shows the species composition of the plots. *P. maritima* seedlings were mapped once a month. After emergence of the seedlings the sowing pattern could generally be recognized quite well. In each zone *P. maritima* seedlings were also counted in reference plots to obtain an impression of spontaneous germination.

RESULTS AND DISCUSSION

The percentages of emerged seedlings and the mortality rate are given in Fig. 11.1 - 11.4. In all plots the first seedlings were visible three weeks after sowing. In the highest-lying zone (series A) germination took place throughout the season. In series B few seedlings emerged except for a small germination wave in August. In series C germination took place soon after sowing. The mortality in series B and C was high, although the plants in series C lived longer than those of series B (plots on a heavily trampled cattle path). The mortality in series C occurred mainly in August. In the dense vegetation layer of series D, relatively many seedlings germinated. Compared with series B and C, series D had low mortality rates. In the reference plots the emergence of *P. maritima* seedlings was very low, the highest numbers being 4 in series A, 2 each in series B and C, and 3 in series D. Frequent observation provided a rather good impression of the causes of seedling mortality in *P. maritima*. In the sandy zone of series A, especially in plots A-1 and A-3, seedlings were regularly excavated by burrowing rabbits. The
results show clearly that in this relatively unfavourable environment the emerged seedlings were able to maintain themselves by rapid growth. In series B the seedlings died off rather soon. This can be ascribed to the intense trampling by cows. Apparently, seedlings of *P. maritima* cannot stand this trampling.

Due to the daily flooding, the soil of series C was marshy. The roots of many seedlings were evidently knocked loose repeatedly. This phenomenon was reinforced by the influence, albeit of low frequency, of the trampling by cows. In the grassy plots of series D the plants were able to maintain themselves relatively well. Just as for series A, a low flooding frequency was apparently not disastrous: in series A and D, plants originating from this sowing experiment were still present at the end of the season. To obtain an impression of the influence of winter conditions and the rate of survival, observation of the plots will be continued in the spring of 1981.
Fig. 11.3. Series C. Germination and mortality of *Plantago maritima* sown near a creek, flooded during each high-tide period.

Fig. 11.4. Series D. Germination and mortality of *Plantago maritima* sown near a creek, flooded only during extremely high tides.

From the results, it may be concluded that the emergence of *P. maritima* seedlings from artificially sown seeds can occur immediately, but the numbers of seedlings are low. Germination can occur in a sandy soil (series A) as well as in muddy soils (series B, C and D). Burrowing and heavy trampling are important causes of mortality, as is daily inundation by seawater. To obtain establishment of *P. maritima*, many seeds have to be released. A seed-bank study might provide information about the amounts of seed necessary for establishment.

REFERENCES