Effects of trampling and soil compaction on the occurrence of some Plantago species in coastal sand dunes

IVa. The vegetation of two dune grasslands in relation to physical soil factors *

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SUMMARY

To study the effects of trampling and soil compaction on the occurrence of four Plantago species, the vegetation of two coastal dune grasslands in the south-western part of the Netherlands has been described. One of these grasslands is grazed by cattle and the other intensively trampled by people.

The distribution of Plantago coronopus, P. lanceolata, P. major ssp. major and P. major ssp. pleiosperma was investigated in relation to the soil characteristics pore volume, resistance, moisture and organic matter.

P. major ssp. major is able to grow in heavily trampled, compacted soils, P. major ssp. pleiosperma occurs mainly under environmental conditions which are unstable due to irregular fluctuations of a high water table.

P. coronopus has been observed in compacted dry soils which are poor in organic matter. Two types of P. lanceolata were distinguished: the first type occurs in the mesosere on moderately trampled sites and the second type can be found on lightly trampled sites in the xerosere.

1. INTRODUCTION

The species composition of many semi-natural grasslands in the coastal areas of the Netherlands is highly influenced by cattle grazing or walking by people. More insight into the factors which are affecting the vegetation is important not only from the ecological point of view but also as regards nature conservation management. Although the influences of cattle grazing

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and walking by people may be rather different (Crisp 1964; Duffey 1967),
common effects of both are trampling and soil compaction.

In this series of papers (Blom 1976, 1977, 1978a, b, 1979 and this paper) a study on the effects of trampling and soil compaction on the occurrence of four *Plantago* species in coastal dune grasslands is described. The *Plantago* species were chosen since the distribution of *P. major* ssp. *major* is thought to be positively correlated with the environmental factors of trampling or soil compaction (e.g. Oberdorfer 1970, 1971). It was considered useful to compare the occurrence of this taxon with that of some closely related species in the same genus and with a similar life form. The study can be divided into three parts, one at the phytosociological level (this paper), the second at the experimental level under field conditions and the third at the experimental level under laboratory conditions. The aim of the experimental studies is to determine in detail the combined and separate effects of trampling and soil compaction on the behaviour of the species during all the stages of their life-cycle. The effects on germination, emergence, seedling establishment, growth and seed production have been published already in previous papers (Blom 1976, 1977, 1978a, b, 1979).

Syntaxonomical investigations of plant communities influenced by grazing or by public pressure have been rendered by many authors (e.g. Boerboom 1957; Ellenberg 1963; van der Maarel 1966a, 1978; Sissingh 1969; Oberdorfer 1971). Other authors studied the reaction of single species or particular communities on these environmental factors (e.g. Goldsmith et al. 1970; Burden & Randerson 1972; Liddle & Greig-Smith 1975b; Blom 1976, 1977, 1978a, b, 1979; Boorman & Fuller 1977; Crawford & Liddle 1977).

In literature, there has been little attempt to synthesize studies at the phytosociological level with studies at the experimental level. With reference to the effects of trampling, the work of Liddle & Greig-Smith (1975b) is one of the few examples in which a phytosociological approach is supported by an experimental approach on a single species (*Festuca rubra*).

This paper is in three sections. Firstly a survey will be given of the plant communities occurring on the “Westduinen”, a more or less intensively grazed dune grassland on the island of Goeree. The aim of this approach is to determine the phytosociological position of *Plantago major* ssp. *major*, *P. major* ssp. *pleiosperma*, *P. lanceolata* and *P. coronopus*.

Secondly, the effects of public pressure on the vegetation of the “Heveringen”, a dune grassland on Voorne (north of Goeree) are also described and compared with the vegetation of similar, but grazed, areas. In the third section attention is paid to the relation between distribution patterns of *Plantago* species in the dune grasslands under study and the soil factors, compaction, moisture and organic matter.

In this series of papers (Blom 1976, 1977, 1978a, b, 1979 and this paper)
an attempt is made to understand the occurrence of *Plantago* species and their communities with the help of experiments under controlled conditions.

2. THE STUDY AREAS

Studies were made of two dune grasslands, on the islands of Voorne and Goeree (the south-west Netherlands). Dune grasslands can be found on the stabilized parts of coastal sand dune areas. Unless the habitat is very poor in lime (Westhoff 1971), they are characterized by a low, dense and species-rich vegetation with a relatively high diversity in structure and many gradients in edaphic factors (see Westhoff 1947; Van der Maarel 1966a, b; Boorman 1977). The landscape of the areas investigated is characterized by low hills with rounded tops, generally not exceeding 6 m above sea level, and shallow slacks formed by blowouts down to the groundwater level. On Goeree, the “Westduinen” is an example of a stabilized grazed dune grassland with a high fluctuating water table; in winter the slacks are waterlogged. From May until October the area (Photo 1) is grazed by cattle and horses (about 60 animals each year on 176 ha). Fertilizers are applied in a small part of the “Westduinen”.

The second dune-grassland complex, the now ungrazed “Heveringen” on Voorne, was extensively grazed until 1930, mainly by goats. This area has been open to the public for about 20 years and during spring and summer the pressure by walkers can be very high. Due to the effects of drainage by local cultivations, the phreatic level of the “Heveringen” is considerably lower than in the “Westduinen”. Only in very wet years are the lowest parts of this area submerged. Rabbits have been observed in both areas, although they are far more numerous in the “Heveringen”. The “Heveringen” belongs to a Nature Reserve owned by the Foundation “Het Zuid-Hollands Landschap”. The “Westduinen” is a private area owned by the Polder Administration of Goeree. More detailed descriptions of the “Westduinen” have been given by Weevers (1940), Westhoff et al. (1961), Blom & Willems (1971), and of the “Heveringen” by Van der Maarel & Westhoff (1964).

3. METHODS

In order to obtain a phytosociological description of the two areas, relevés were made according to the Braun-Blanquet approach (Braun-Blanquet 1964) with the refinements proposed by Barkman et al. (1964). To cover the greater part of the vegetation types of the “Westduinen”, 18 transects were chosen in which a total of 150 relevés were made. In the “Heveringen”, 16 transects with 150 plots have been analysed. Following the methods as described by Shimwell (1971), Westhoff & Van der Maarel (1973), Mueller-Dombois & Ellenberg (1974), and Moravec (1978) the relevés were aggregated in primary tables transect by transect for each area and then rearranged in synoptic tables, which are presented in this paper.
Photo 1. The "Westduinen" on Goeree.
To obtain insight into the effects of trampling on the physical characteristics of the soil, a number of soil factors were determined. At each relevé (4 m²) two soil samples (depth 1–6 cm) were collected in order to determine the organic matter and the soil-moisture content. To get an impression of the compaction of the soil, resistance was determined by means of a penetrometer (each relevé 10 measurements at 5 and 10 centimetres below soil surface). The pore volumes from 3 to 7 centimetres below the soil surface were also determined with a vacuum air pycnometer according to Langer (three measurements per site). In a part of the “Westduinen” the factors mentioned were measured at random points to analyse the distribution of *P. lanceolata* in relation to physical soil factors. The results of the latter investigations will be published in a later paper (Noë & Blom, in preparation).

For the nomenclature of the higher plants the Flora of the Netherlands (Heukels & Van Ooststroom 1975) is followed. The mosses have been identified with Margadant (1959), and the lichens with Hennipman & Sipman (1978), Duncan (1970), and Poelt (1969). If the plant communities described (coena) correspond with certain syntaxa in the Braun-Blanquet system (cf. Westhoff & Den Held 1969), these syntaxa are mentioned for the respective communities. For certain communities, no syntaxon is mentioned. This indicates that the coenon concerned is transitional between different syntaxa.

4. RESULTS

A. The vegetation of the “Westduinen” on Goeree

Due to differences in level between the ground water and the soil surface, the vegetation of the “Westduinen” can be divided into communities belonging to the hygrosere, with species growing on mostly water-saturated soils, to the mesosere with species occurring on soils that are moderately wet as a result of capillary rise, and the xerosere with plants growing on relatively dry soils. According to Londo (1971) the species of the hygrosere and the mesosere can be taken together as phreatophytes. Since the “Westduinen” is characterized by a fluctuating groundwater level, the wet areas present a more dynamic (with reference to the factor soil moisture: unstable) character than the humid or dry sites. Firstly, the coena of the hygrosere and the mesosere will be described. The relevés are arranged in a synoptic table (Table 1). Secondly, the coena of the xerosere will be described (Table 2). A survey of the probable relationships between these coena is given in Scheme 1. Soil characteristics of the various coena are given in Table 4a and 4b.

**Description of the coena from the hygro- and mesosere (Table 1)**

**COENON 1. Community of Potentilla anserina and Agrostis stolonifera**

On the “Westduinen” this coenon can be found in the lower parts of
TABLE 2. Synoptic table of the xerosere of the "Westdulmen"

<table>
<thead>
<tr>
<th>Coenon</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
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<td></td>
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<tr>
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<td></td>
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<tr>
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<tr>
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Addenda: Erodium glutinosum 10(6, 5) Ornithopus perpusillus 13(16, 1-1)
Eryngium campestre 12(19, +1) Cerastium holostoides 13(10, +1)
Brya media 13(25, +1) Geranium molle 13(20, +1)
the slacks. The sandy soil is rich in organic matter and due to a high fluctuating phreatic level it is mostly water saturated (Table 4a). This coenon belongs to the alliance Agropyro-Rumicion crisp; the observed character- and differential species are Potentilla anserina, Leontodon autumnalis, Juncus articulatus, Agrostis stolonifera, and Ranunculus repens. Plantago major ssp. pleiosperma occurred in half the relevés and locally P. major ssp. major was found.

COENON 2. Community of Centunculus minimus and Juncus bufonius

This coenon occurs on sites in wet slacks which are heavily trampled by cattle and have thus, the greater part, bare soil. Due to the low organic matter content the water availability and the soil resistance are relatively low (Table 4a). The low values of the pore volume are an indication of the intensive trampling activities on these sites. This coenon represents a number of character- and differential taxa of the alliance Nanocyperion flavescentis, viz. Gnaphalium uliginosum, Juncus bufonius, Centunculus minimus and Radiola linoides (see Table 1). Furthermore, in all relevés P. major ssp. pleiosperma was observed.

COENON 3. Community of Carex serotina and Salix repens

Besides the two species mentioned above this coenon is characterized by the occurrence of Eurhynchium praelongum, Fissidens adiantoides, Carex trinervis, Hydrocotyle vulgaris, and Galium uliginosum. This coenon can be found in the higher sites in the slacks and the floristic composition depends on the grazing intensity as well as on the distance between the groundwater table and the soil surface (cf. Van der Laan 1979). At increasing grazing pressure, Salix repens disappears, whereas Carex serotina is resistant to trampling by cattle. A relatively high organic matter content has been measured. Due to the dense root layer, the pore volume values are relatively high (Table 4a). The sites on which this coenon can be found are submerged in wet winters.

COENON 4. Community of Gentianella campestris and Linum catharticum

Besides the above mentioned two species, Gentianella amarella and Carex panicea are also important species within this coenon. Two separate habitats in which this coenon occurs can be distinguished (Table 4a). The first one is characterized by a high moisture level and a high organic matter content. Grazing is nearly absent, resulting in a relatively high pore volume. The second one is much drier; the organic matter content appeared to be low and the soil is lightly trampled resulting in a lower pore volume.

COENON 5. Community of Sieglingia decumbens and Viola canina

This coenon is present on sites which dry up relatively quickly during the summer. In winter the soil is moist but not submerged. The grazing intensity on these sites is generally high, resulting in a low vegetation layer,
a low organic matter content, a relatively low pore volume and a high soil resistance (Table 4a).

This coenon belongs to the alliance Violion caninae and the observed character species are the two above mentioned species with *Euphrasia officinalis* and *Polygala vulgaris*. Locally *Botrychium lunaria* was found.

Lower trampling intensities result in less compacted soils with a decrease in capillary rise. On such sites, species of the xerosere invade. Such stands can be considered as a transition to the xerosere.

**COENON 6. Community of *Spiranthes spiralis* and *Briza media***

This coenon is characterized by the combination of the species *Spiranthes spiralis*, *Briza media* and *Carex flacca*. Its occurrence is limited to gradients at the edges of slacks with a high moisture content in winter but a relatively low moisture level in summer. These moderately grazed sites represent zones between the meso- and xeroseres.

**COENON 7. Community of *Prunella vulgaris* and *Luzula campestris***

This coenon occurs on fertilized sites of the "Westduinen". The human impact (fertilizing) can be considered as the major factor in determining the floristic composition of the vegetation. The influence of the large spread in moisture content (Table 4a) will be relatively small. Differences in grazing intensities have been observed. In general this coenon can be considered as a transition between the coena 5, 6, and 8 of the mesosere.

**COENON 8. Community of *Lolium perenne* and *Holcus lanatus***

This coenon can be found on sites with a high grazing intensity, and belongs to the Poo-Lolietum (alliance Agropyro-Rumicion crispi). The following character- and differential species were observed: *Trifolium repens*, *Ranunculus repens*, *Lolium perenne*, *Taraxacum sect. Vulgaria* and *Plantago major ssp. major*. Due to a relatively high organic matter content, the pore volume values are in general moderate. Only on very intensively trampled sites are the pore volume values very low. *P. major ssp. major*, *Trifolium repens* and *Taraxacum sect. Vulgaria* are resistant to these heavy trampling regimes (see Section C of this paper).

**Description of the coena from the xerosere of the “Westduinen” (Table 2 and Scheme 1)**

In the xerosere the Airo-Caricetum arenariae, described by, for example, Westhoff et al. (1961), Van der Maarel (1966a), and Westhoff & Den Held (1969), is represented in the coena 10 to 14.

The differences in structure and floristic composition between the coena are caused partly by variations in aspect of the soil surface and, thus, by the microclimatological differentiation. Furthermore, differences are due to various degrees of soil compaction resulting in differences in moisture availability (Blom 1976). The trampling intensity appeared to be important
## TABLE 1. Synoptic table of the hygrosere and mesosere of the "Westduinen"

<table>
<thead>
<tr>
<th>Coenon</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
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</tr>
</thead>
<tbody>
<tr>
<td>No. of relevés</td>
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<td>9</td>
<td>6</td>
<td>11</td>
<td>16</td>
<td>9</td>
<td>11</td>
<td>4</td>
</tr>
</tbody>
</table>

- **Cynosurus cristatus**
- **Agrostis canina**
- **Salix repens**
- **Juncus bufonius**
- **Carex serotina**
- **Plantago major ssp. pleiosperma**
- **Gentianella campestris**
- **Aira praecox**
- **Viola canina**
- **Brachythecium albicans**
- **Beilis perennis**
- **Carex fiacca**
- **Lotus corniculatus**
- **Leontodon nudicaulis**
- **Galium verum**
- **Plantago lanceolata**
- **Equisetum arvense**
- **Coenon**

### Notes

- The percentages and cover of the species are given between the brackets. The other figures indicate the number of the coena in which the species were found.
for the establishment of seedlings as demonstrated for the *Plantago* species by Blom (1977). Other factors inducing differences in the floristic assemblage of the vegetation are the organic matter content of the soil and the degree of stability or instability due to differences in grazing frequencies during the year and between several years.

**Coenon 9. Community of Tortula ruralis and Phleum arenarium**

This coenon is identical with the association Tortulo-Phleum arenarii. It can be observed on sites with a high degree of rabbit grazing which induces an open vegetation. The organic matter content and the moisture level are very low as are the penetrometer values; the value of pore volume is relatively high (Table 4b).

**Coenon 10. Community of Corynephorus canescens and Cornicularia aculeata**

The greater part of the neutral to mildly acid and loose soil on which this coenon can be found, is covered by *Corynephorus canescens* accompanied by *Cornicularia aculeata* and several *Cladonia* species. This coenon occurs mostly on south-facing slopes and the soil dynamics result in a small amount of organic matter.

On tops of small dunes on which sand movements are frequent, and on steep slopes exposed to the south an open *Corynephorus*-variant can be found. In this variant, besides *Corynephorus canescens* few species of coenon
9 are able to germinate and to establish themselves. Depending on the reaction of the soil the open *Corynephorus*-variant may fade into the coena 9 or 10. These coena can be considered as transitions to the alliance Galio-Koelerion.

**COENON 11. Community of Lecidea granulosa and Cladonia glauca**

This coenon is characterized by dead tussocks of *Corynephorus canescens*, frequently present on the steep south-facing slopes. On these dead tussocks, *Lecidea granulosa* and *L. uliginosa* are growing. Furthermore, many *Cladonia* species, *Aira praecox* and *Rumex acetosella* occur on these sites, where grazing is nearly absent. On the open sites within this environment, several species of winter annuals are able to complete their life-cycle while the land is not being grazed by cattle. These species (e.g. *Arenaria serpyllifolia*, *Cardamine hirsuta*, *Cerastium semidecandrum*, *Erophila verna* and *Saxifraga tridactylites*) are very vulnerable to trampling.

**COENON 12. Community of Dicranum scoparium and Jasione montana**

This coenon occurs as a terminal vegetation on ungrazed steep slopes exposed to the north. A prerequisite for a development to this vegetation is a relatively dry and slightly acid soil. Besides the species which have been mentioned, *Carex arenaria*, *Anthoxanthum odoratum* and *Hygrochaeris radicata* are also frequently present on these sites.

**COENON 13. Community of Thymus pulegioides and Ononis repens**

This coenon can be assigned to the alliance Galio-Koelerion and proceeds from the coena mentioned in the xerosere as the grazing intensity increases on soils rich in organic matter (Table 4b). The vegetation cover is more closed than in the previous coena. However, due to trampling by grazing animals a number of winter annuals, character species of the order Festuco-Sedetalia are represented on small open areas. From the evidence of the floristic assemblage (*Thymus pulegioides*, *Ononis repens* and *Helictotrichon pubescent*) the substrate would seem to be mildly alkaline. The occurrence of *Sieglungia decumbens* indicates the alliance Violion caninae.

**COENON 14. Community of Vicia lathyroides and Aphanes microcarpa**

This coenon has its optimal occurrence on small open sites with a low organic matter content within coenon 13. Character species of the order Festuco-Sedetalia, which are also locally differential, are *Vicia lathyroides*, *Teesdalia nudicaulis*, *Trifolium campestre*, *Aira praecox* and *Sedum acre*. Moreover, *Trifolium dubium*, *T. micranthum* and *T. scabrum* are local differential species.

**COENON 15. Community of Plantago coronopus and Bellis perennis**

On sites previously disturbed by rabbits and afterwards intensively trampled by cattle this coenon occurs. This coenon is characterized by the
high frequency of *Plantago coronopus*, *Bellis perennis*, *Lolium perenne*, *Rhytidiadelphus squarrosus*, *Ranunculus bulbosus* and *Cynodon dactylon*. Since these sites can be found mostly in lows, the water content of the soil is relatively high (Table 4b). Due to the intense trampling during the grazing season, the soil is relatively compact.

B. The vegetation of the “Heveringen” on Voorne

The greater part of the vegetation of the “Heveringen” belongs to the Festuco-Galietum maritimi, an association with a large variation in species composition (Van der Maarel, 1966a).

Compared with the xerosere of the “Westduinen” the soil is dry (cf. Table 4b and 4c). The variation in the floristic assemblage is due to differences in trampling intensities, which influence the compaction of the soil (see Table 4c, penetrometer values and pore volumes). Furthermore, the differing aspects as well as the reaction of the soil (from mildly alkaline to mildly acid) cause differences in the composition of the vegetation. Grazing by rabbits and trampling by walkers are important factors preventing a further succession of the vegetation in the greater part of the “Heveringen”.

A description of the coena will be given and a comparison will be made between the coena of the “Heveringen” and those of the xerosere in the “Westduinen”. In Scheme 2, the probable relationship between the coena on the “Heveringen” will be presented.

Description of the coena on the “Heveringen” and a comparison with the vegetation occurring in the xerosere of the “Westduinen” (Table 3 and Scheme 2).

Many small sites on the “Heveringen” are characterized by an open soil layer and thus by bare sand. These sites are mostly conditioned by the impact of children playing on south-facing slopes. If there is frequent disturbance, only *Carex arenaria* is able to grow on these sites. If the disturbance is only incidental, for example during one summer, the establishment of *Corynephorus canescens* takes place. Both species are accompanied by a few winter annuals (e.g. *Erophila verna*) and these variants are comparable with the open *Corynephorus*-variant of the “Westduinen” (see coenon 10). The *Corynephorus*-variant on the “Heveringen” is limited to the tops of hills, whereas *Carex arenaria* frequently grows on the slopes. The latter variant in particular can develop into the coenon first described.

**COENON 1. Community of Senecio jacobaea and winter annuals**

This coenon can be observed on open and loose soils with slight movement of sand and belongs to the Tortulo-Phleetum arenarii. As described by Janssen (1972, 1973a, b) the edaphic conditions of these sites are ap-
<table>
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<tr>
<th>Coenon</th>
<th>1</th>
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<th>3a</th>
<th>3b</th>
<th>4a</th>
<th>4b</th>
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**TABLE 3. Synoptic table of the "Heveringen"**

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<th>3b</th>
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**Addenda:**

- Brachycheilum albidum
- Rhaconitron canescens
- Pseudoceratium purum
- Lecidea uliginosa
- Amano sp. sylvipilosa
- Hipposphyx rhamnoides (juv.)
- Veronica serpyllifolia
- Vicia lathyroides

**Communities of the "Heveringen"**

- Community of Carex flacca
- Community of Galium verum
- Community of Hypochaeris radicata
- Community of Plantago lanceolata
- Community of Agrostis tenus
- Community of Rumex acetosella
- Community of Luzula campestris
- Community of Achillea millefolium
- Community of Rhodiola dictyoneura squarrosa
- Community of Melilotus pubescens
- Community of Potentilla erecta

**Communities of the "Heveringen" with a"n"**

- Community of Carex flacca
- Community of Galium verum
- Community of Hypochaeris radicata
- Community of Plantago lanceolata
- Community of Agrostis tenus
- Community of Rumex acetosella
- Community of Luzula campestris
- Community of Achillea millefolium
- Community of Rhodiola dictyoneura squarrosa
- Community of Melilotus pubescens
- Community of Potentilla erecta

**Communities of the "Heveringen" with a "b"**

- Community of Carex flacca
- Community of Galium verum
- Community of Hypochaeris radicata
- Community of Plantago lanceolata
- Community of Agrostis tenus
- Community of Rumex acetosella
- Community of Luzula campestris
- Community of Achillea millefolium
- Community of Rhodiola dictyoneura squarrosa
- Community of Melilotus pubescens
- Community of Potentilla erecta

**Communities of the "Heveringen" with a "c"**

- Community of Carex flacca
- Community of Galium verum
- Community of Hypochaeris radicata
- Community of Plantago lanceolata
- Community of Agrostis tenus
- Community of Rumex acetosella
- Community of Luzula campestris
- Community of Achillea millefolium
- Community of Rhodiola dictyoneura squarrosa
- Community of Melilotus pubescens
- Community of Potentilla erecta

**Communities of the "Heveringen" with a "d"**

- Community of Carex flacca
- Community of Galium verum
- Community of Hypochaeris radicata
- Community of Plantago lanceolata
- Community of Agrostis tenus
- Community of Rumex acetosella
- Community of Luzula campestris
- Community of Achillea millefolium
- Community of Rhodiola dictyoneura squarrosa
- Community of Melilotus pubescens
- Community of Potentilla erecta

**Communities of the "Heveringen" with a "e"**

- Community of Carex flacca
- Community of Galium verum
- Community of Hypochaeris radicata
- Community of Plantago lanceolata
- Community of Agrostis tenus
- Community of Rumex acetosella
- Community of Luzula campestris
- Community of Achillea millefolium
- Community of Rhodiola dictyoneura squarrosa
- Community of Melilotus pubescens
- Community of Potentilla erecta

**Addenda:**

- Brachycheilum albidum
- Rhaconitron canescens
- Pseudoceratium purum
- Lecidea uliginosa
- Amano sp. sylvipilosa
- Hipposphyx rhamnoides (juv.)
- Veronica serpyllifolia
- Vicia lathyroides

**Communities of the "Heveringen" with a "f"**

- Community of Carex flacca
- Community of Galium verum
- Community of Hypochaeris radicata
- Community of Plantago lanceolata
- Community of Agrostis tenus
- Community of Rumex acetosella
- Community of Luzula campestris
- Community of Achillea millefolium
- Community of Rhodiola dictyoneura squarrosa
- Community of Melilotus pubescens
- Community of Potentilla erecta
propriate for the germination and establishment of many winter annuals. This coenon is equivalent to coenon 9 (Tortula with Phleum) of the “Westduinen”.

COENON 2. Community of Hypnum cupressiforme and Rumex acetosella

This coenon differs from coenon 1 by a denser layer of Hypnum cupressiforme and, for example, the occurrence of Plantago lanceolata and Agrostis tenuis. Compared with the other coena no differential species were observed. Due to a high trampling intensity, the resistance of the upper soil layers is high and the value of pore volume low. This coenon, too, corresponds to a certain degree with coenon 9 of the “Westduinen”. This community can be considered as the terminal phase of the Tortulo-Phleetum arenarii and is a transition to the Festuco-Galietum maritimi.

COENON 3a. Community of Hypnum cupressiforme and Corynephorus canescens

COENON 3b. Community of Cladonia foliacea and Corynephorus canescens

On loose soils with slight movements of sand the open Corynephorus-variant develops into coenon 3a. On sites with a fully stabilized soil the lichens Cladonia furcata and C. foliacea are able to become established (coenon 3b). During certain short periods of the year, moderate trampling is observed on these sites. The recovery of the vegetation occurs relatively quickly. Both communities are transitions between the Festuco-Galietum maritimi and the Violo-Corynephoretum. Fragments of the Tortulo-
Phlegetum arenarii are represented in coenon 3a. Both coena correspond with coenon 10 (Corynephorus with Cornicularia) of the “Westduinen”.

**COENON 4a. Community of Festuca ovina and Galium verum**

**COENON 4b. Community of Thymus pulegioides and Taraxacum rubicundum**

**COENON 4c. Community of Sieglingica decumbens and Hieracium pilosella**

These three coena represent the Festuco-Galietum maritimi. Coenon 4a can be considered as a typical variant (no differential species). Coenon 4b is characterized by the differential species *Thymus pulegioides, Taraxacum rubicundum* and *Polygala vulgaris*. This community occurs on mildly alkaline soils (Scheme 2) and is a transition to the Taraxaco-Galietum maritimi. Coenon 4c is a transition to the alliance Violion caninae. These communities are characterized by a closed vegetation layer on a soil relatively rich in organic matter (Table 4c). Intense grazing by rabbits prevents a further succession. Furthermore, intense trampling by walkers has been observed. These coena correspond with coenon 13 (*Thymus* with *Ononis*) of the “Westduinen”.

**COENON 5. Community of Rosa pimpinellifolia and Crataegus monogyna**

This coenon can be found on the edges of communities mainly consisting of large shrub layers with *Crataegus monogyna* and *Hippophae rhamnoides*. Due to the grazing activities of rabbits the vegetation layer of this coenon is low and the development into a shrub vegetation is inhibited. The vegetation is scarcely trampled by people and no corresponding coenon exists on the “Westduinen”.

**COENON 6. Community of Dicranum scoparium and Cladonia glauca**

This coenon can be found on dry north-facing slopes. The environmental conditions and the composition of the vegetation are equivalent to those of coenon 12 (*Dicranum* with *Jasione*) of the “Westduinen”.

**COENON 7. Community of Holcus lanatus and Leontodon autumnalis**

This coenon establishes itself on relatively humid sites, mostly from coenon 4e as trampling increases or from coenon 4b as grazing by rabbits decreases. No comparison with the “Westduinen” is apparent.

**COENON 8. Community of Plantago coronopus and Potentilla erecta**

This coenon can be observed on sites heavily trampled in summer. The relatively dry soil is compacted (Table 4e). This vegetation is species rich and in the “Westduinen” no comparable site can be found.

**COENON 9. Community of Calamagrostis epigejos and Elytrigia repens**

This coenon occurs on disturbed sites, for example on the edges of bridle-paths. The sandy soil of these sites is dry and relatively loose. On the “Westduinen” this coenon is absent.

*(To be continued)*

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Effects of trampling and soil compaction on the occurrence of some Plantago species in coastal sand dunes

IVb. The vegetation of two dune grasslands in relation to physical soil factors *

by C. W. P. M. Blom, L. M. F. Husson and V. Westhoff

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Department of Botany, University of Nijmegen

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C. Trampling and related soil factors

The values of soil resistance, pore volume, moisture content and content in organic matter as measured in the “Westduinen” and the “Heveringen” are given in Table 4. Lowest values of soil resistance have been observed on sites belonging to the xerosere of the “Westduinen”. These sites are scarcely or lightly trampled; the soil is dry and poor in organic matter and the vegetation layer is open. The soils in the wetter parts of the “Westduinen” are moderately or heavily trampled; the values for soil resistance are higher on these sites than on the dry ones (Table 4a and 4b). In spite of the higher trampling intensities on these wet soils, which are in general rich in organic matter, the pore volumes are high. The soil resistances of the “Heveringen” appeared to be higher than those of the “Westduinen” (Table 4c). Lower values in pore volume are also found in the “Heveringen”. The soil is dry and the values in organic matter were in general between those of the xerosere and hygro- and mesosere of the “Westduinen”.

To get an impression of the relation between the distribution of the Plantago species and the soil characteristics of resistance, pore volume, moisture content and organic matter, a transect in the “Westduinen” has been studied in detail (Fig. 1 and Table 6). In addition to a description of the vegetation the occurrence of individuals of the Plantago species

* Grassland Species Research Group Publication No. 9.
Fig. 1. The distribution of three *Plantago* species in a transect perpendicular to a heavily trampled cattle path in the dune grassland "Westduinen" (see also Tabel 6). Size of symbols indicates size of individual plants.

has been mapped (Fig. 1) This transect was chosen perpendicular to a heavily trampled cattle path in the neighbourhood of a drinking pool. The vegetation of the edges of the path (B₁, B₃) belongs to coenon 8 (*Lolium perenne* with *Holcus lanatus*). The soil in the middle of the path (B₂) was relatively bare; only some individuals of *Plantago major* ssp.
major, Taraxacum sect. Vulgaria, Trifolium repens, Leontodon autumnalis and Sieglingia decumbens were found. The stand of the south-west facing slope (A) can be considered as belonging to coenon 13 (Thymus pulegioides with Ononis repens) and those of the north-east facing slope (C) to coenon 15 (Plantago coronopus with Bellis perennis).

The soil in the middle of the path (B2) was strongly compacted (Table 6); in comparison with the other sites on the “Westduinen”, the resistance of the soil appeared to be very high and the value of the pore volume low. Rain water did not penetrate the compacted soil; on wet days puddles were observed. In comparison with the edges (B1 and B3) the soil resistance and the pore volume values appeared to be low on the slopes (A and C). This phenomenon has been also observed on other slopes of the “Westduinen” and “Heveringen” (for example Table 4c, coena 3b and 6). Relatively small differences in organic matter were found between the various sites. The moisture content of the soil of the edges (B1, B3) was much higher than on the other sites. As shown in Fig. 1 P. major ssp. major occurred frequently on the path and to a lesser extent on the edges. P. lanceolata was frequently observed on slope A, whereas P. coronopus occurred in greater numbers on slope C.

5. DISCUSSION

In this paper, an attempt is made to study the occurrence of three Plantago species and their presence in various communities in relation to, mainly physical, soil factors in low trampled dune grasslands in the Netherlands. To get an impression of the large scale distribution of the Plantago species the Braun-Blanquet approach has been applied. P. major ssp. pleiosperma occurs on wet, compacted soils (coenon 2, Table 4a). This taxon can be found in communities belonging to the Nanocyperion flavescentis and the Agropyro-Rumicion crispi (Table 1, coena 2 and 1, respectively). In the “Heveringen” this taxon was only observed at one moist site along an artificial pond. The edaphic conditions of that site were equivalent to those of coenon 2 (Table 4a) of the “Westduinen”. P. major ssp. major has been observed mostly on paths with an open vegetation layer belonging to the Poo-Lolietum (Table 1, coenon 8 and Fig. 1). The compacted soil of these sites was moderately wet and rich in organic matter (Table 4a). According to Molgaard (1976) it can be stated that P. major ssp. pleiosperma is able to grow under more unstable environmental conditions than P. major ssp. major. This unstable condition is mainly due to irregular fluctuations in the high water table. It should be noticed that with reference to the possible occurrence of different genotypes within one single species (Groot & Boschhuizen 1970; Wu & Antonovics 1976) various populations of a species must be studied in order to characterize the reaction of that species on certain environmental conditions. On the “Westduinen” P. coronopus has been observed on relatively dry soils, which are poor in organic matter and relatively compact. These sites have
Table 4a. Soil data for the coena of the hygro- and mesosere of the "Westduinen"

<table>
<thead>
<tr>
<th>Coenon</th>
<th>*</th>
<th>Soil resistance (kg/cm²)</th>
<th>Pore volume (% S.E.)</th>
<th>Soil moisture (% by dry weight S.E.)</th>
<th>Organic matter (% loss of ignition S.E.)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>5 cm S.E.</td>
<td>10 cm S.E.</td>
<td>5 cm S.E.</td>
<td>10 cm S.E.</td>
</tr>
<tr>
<td>1. Potentilla with Agrostis</td>
<td>P</td>
<td>14.7 ± 1.2</td>
<td>16.7 ± 0.6</td>
<td>73.8 ± 4.4</td>
<td>96.3 ± 20.5</td>
</tr>
<tr>
<td>2. Centunculus with Juncus</td>
<td>P+</td>
<td>6.1 ± 1.2</td>
<td>11.2 ± 1.1</td>
<td>54.4 ± 0.7</td>
<td>50.6 ± 8.1</td>
</tr>
<tr>
<td>3. Carex with Salix</td>
<td></td>
<td>11.5 ± 0.5</td>
<td>16.2 ± 0.7</td>
<td>78.8 ± 3.3</td>
<td>78.0 ± 6.9</td>
</tr>
<tr>
<td>4. Gentianella with Linum</td>
<td>1</td>
<td>12.1 ± 0.5</td>
<td>17.4 ± 0.7</td>
<td>70.1 ± 59.5</td>
<td>59.5 ± 3.4</td>
</tr>
<tr>
<td>5. Sieglingia with Viola</td>
<td></td>
<td>17.9 ± 0.6</td>
<td>19.2 ± 0.4</td>
<td>59.6 ± 2.1</td>
<td>15.9 ± 0.9</td>
</tr>
<tr>
<td>6. Spiranthes with Briza</td>
<td>1+</td>
<td>13.6 ± 0.7</td>
<td>14.6 ± 0.8</td>
<td>68.5 ± 2.5</td>
<td>38.3 ± 6.7</td>
</tr>
<tr>
<td>7. Prunella with Luzula</td>
<td>1</td>
<td>12.4 ± 0.8</td>
<td>16.2 ± 0.8</td>
<td>71.5 ± 4.3</td>
<td>52.6 ± 9.0</td>
</tr>
<tr>
<td>8. Lolium with Holeus</td>
<td>1, m</td>
<td>17.0 ± 1.1</td>
<td>18.2 ± 1.3</td>
<td>64.0 ± 1.8</td>
<td>49.5 ± 10.7</td>
</tr>
</tbody>
</table>

* The presence of Plantago major ssp. pleiosperma within a community is indicated by p, that of P. major ssp. major by m and of P. lanceolata by l. The addition of + means that the taxon concerned has been observed in more than half the relevés. Incidental occurrences of a species are not mentioned (cf. Table 1).
Table 4b. Soil data for the coena of the xerosere of the “Westduinen”

<table>
<thead>
<tr>
<th>Coenon</th>
<th>*</th>
<th>Soil resistance (kg/cm²)</th>
<th>Pore volume (% by dry weight)</th>
<th>Soil moisture (% by dry weight)</th>
<th>Organic matter (% loss of ignition)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>5 cm</td>
<td>10 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9. Tortula with Phleum</td>
<td></td>
<td>5.0 ± 0.9</td>
<td>6.4 ± 0.8</td>
<td>67.4 ± 1.4</td>
<td>3.7 ± 0.3</td>
</tr>
<tr>
<td>10. Corynephorus with Corniculararia</td>
<td></td>
<td>5.4 ± 0.6</td>
<td>9.0 ± 0.5</td>
<td>62.0 ± 1.5</td>
<td>3.0 ± 1.3</td>
</tr>
<tr>
<td>11. Lecidea with Cladonia</td>
<td></td>
<td>9.0 ± 0.5</td>
<td>11.2 ± 0.8</td>
<td>66.3 ∼</td>
<td>10.4 ± 1.0</td>
</tr>
<tr>
<td>12. Dieranum with Jasione</td>
<td></td>
<td>10.0 ± 0.7</td>
<td>12.0 ± 0.5</td>
<td>61.0 ± 2.1</td>
<td>12.9 ± 1.2</td>
</tr>
<tr>
<td>13. Thymus with Ononis</td>
<td>1+</td>
<td>15.8 ± 0.8</td>
<td>14.8 ± 0.6</td>
<td>59.6 ± 2.1</td>
<td>11.9 ± 1.1</td>
</tr>
<tr>
<td>14. Vicia with Aphanes</td>
<td></td>
<td>5.2 ± 0.6</td>
<td>12.8 ± 1.6</td>
<td>∼</td>
<td>3.3 ± 1.0</td>
</tr>
<tr>
<td>15. Plantago with Bellis</td>
<td>1+</td>
<td>13.9 ± 2.0</td>
<td>15.5 ± 1.7</td>
<td>60.3 ± 1.1</td>
<td>17.6 ± 1.1</td>
</tr>
<tr>
<td></td>
<td>c+</td>
<td>∼</td>
<td>∼</td>
<td>∼</td>
<td>∼</td>
</tr>
</tbody>
</table>

— no value available

* 1+, c+: *Plantago lanceolata* and *P. coronopus* respectively, were observed in the greater part of the relevés of the community concerned (cf. Table 2).
Table 4c. Soil data for the coena of the "Heveringen"

<table>
<thead>
<tr>
<th>Coenon</th>
<th>Soil resistance (kg/cm²)</th>
<th>Pore volume (%)</th>
<th>Soil moisture (% by dry weight)</th>
<th>Organic matter (% loss of ignition)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5 cm</td>
<td>10 cm</td>
<td></td>
<td>5 cm</td>
</tr>
<tr>
<td></td>
<td>x</td>
<td>S.E.</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>1.  Senecio with winter annuals</td>
<td>12.1  0.8</td>
<td>12.6  0.4</td>
<td>67.8  0.8</td>
<td>1.7  0.2</td>
</tr>
<tr>
<td>2.  Hypnum with Rumex</td>
<td>23.3  1.6</td>
<td>20.9  1.6</td>
<td>53.4  —</td>
<td>4.3  0.7</td>
</tr>
<tr>
<td>3a. Hypnum with Corynephorus</td>
<td>15.3  1.5</td>
<td>16.2  1.2</td>
<td>54.0  2.2</td>
<td>2.4  0.4</td>
</tr>
<tr>
<td>3b. Cladonia with Corynephorus</td>
<td>22.9  1.7</td>
<td>17.7  0.6</td>
<td>48.6  —</td>
<td>0.7  0.1</td>
</tr>
<tr>
<td>4a. Festuca with Galium</td>
<td>23.2  1.0</td>
<td>22.8  0.9</td>
<td>55.7  1.5</td>
<td>2.1  0.3</td>
</tr>
<tr>
<td>4b. Thymus with Taraxacum</td>
<td>22.7  1.1</td>
<td>20.8  0.7</td>
<td>56.7  1.0</td>
<td>3.8  0.4</td>
</tr>
<tr>
<td>4c. Sieglinga with Hieracium</td>
<td>21.8  1.0</td>
<td>24.3  0.8</td>
<td>59.1  2.4</td>
<td>4.2  0.4</td>
</tr>
<tr>
<td>5.  Rosa with Crataegus</td>
<td>18.6  1.9</td>
<td>18.0  1.1</td>
<td>63.3  1.5</td>
<td>4.5  0.4</td>
</tr>
<tr>
<td>6.  Dicranum with Cladonia</td>
<td>17.2  1.8</td>
<td>16.7  0.1</td>
<td>52.4  0.6</td>
<td>1.4  0.3</td>
</tr>
<tr>
<td>7.  Holcus with Leontodon</td>
<td>22.0  2.0</td>
<td>27.3  1.8</td>
<td>61.0  1.0</td>
<td>6.4  1.4</td>
</tr>
<tr>
<td>8.  Plantago with Potentilla</td>
<td>22.6  0.6</td>
<td>22.5  0.5</td>
<td>53.8  1.1</td>
<td>3.7  0.4</td>
</tr>
<tr>
<td>9.  Calamagrostis with Elytrigia</td>
<td>16.6  0.9</td>
<td>17.7  0.4</td>
<td>66.9  —</td>
<td>3.3  0.4</td>
</tr>
</tbody>
</table>

— no value available

* The presence of Plantago lanceolata within a community is indicated by 1, that of P. coronopus by c. The addition of + means that the taxon concerned has been observed in more than half the relevés.
been frequently disturbed by rabbits (Table 2, coenon 15). Most species belong to the Airo-Caricetum arenariae or the Galio-Koelerion. Observations in other years demonstrated that especially in the case of \textit{P. coronopus} strong fluctuations in numbers of individuals occurred, which was also observed for a number of other species by Watt (1960, 1971), Westhoff (1969), Van der Laan (1979), and J. P. van den Bergh (personal communication). On the “Heveringen” \textit{P. coronopus} is mostly observed on paths which are heavily trampled in summer (Table 3, coenon 8 and Table 4c). In a part of the “Heveringen” \textit{P. coronopus} occurs in a community forming a transition between the Nanocyperion flavescentis and the Galio-Koelerion (cf. Van der Maarel 1966b, 1978). Onyekwelu (1972a, b) stated that the establishment of \textit{P. coronopus} on wet sites in the dunes of North Wales was limited by the lack of nitrogen and phosphorus; the establishment at low water tables is much better (cf. Table 4b, c).

\textit{P. lanceolata} has been observed in considerably more relevés than the other \textit{Plantago} species (Table 1, 2, and 3). In the mesosere of the “Westduinen” \textit{P. lanceolata} occurs frequently in stands belonging to the alliances Agropyro-Rumicion crispi, Violion caninae and Arrhenatherion elatioris (Table 1). In the xerosere of the “Westduinen” as well as in the “Heveringen” \textit{P. lanceolata} occurs in coena belonging to the Galio-Koelerion and the Thero-Airion (Table 2 and 3). The latter individuals have been determined as \textit{P. lanceolata} var. \textit{sphaerostachya} Mert. and Koch. Also the results of the soil analysis strongly indicate a disjunct distribution pattern of \textit{P. lanceolata} (Table 5). This phenomenon was also observed by Kruijne et al. (1967) in inland grasslands. The first type occurs on humid sites relatively rich in organic matter and a high pore volume, whereas the second type (\textit{P. lanceolata} var. \textit{sphaerostachya}) can be found on dry sites poor in organic matter and with a low pore volume. Since the results presented in this paper are obtained from relatively large plots, only general indications are possible of the relation of a particular species to certain environmental factors. However, the results as presented in Table 5 correspond to findings which will be given in a later paper (Noé & Blom, in preparation). In that paper the relation between the occurrence of \textit{P. lanceolata} and a number of soil factors, as obtained in randomly chosen small plots will be reported; significant differences between two groups of \textit{P. lanceolata} plants were found.

Due to grazing by cattle the development of shrubs is limited in the “Westduinen”. \textit{Salix repens} occurs only on lightly grazed sites (Table 1). On the “Heveringen” communities with shrubs were more frequently observed (Table 3). In this area even \textit{Salix repens} and \textit{Rosa pimpinellifolia} are able to colonize newly exposed soil (cf. Ranwell 1959, 1960).

Due to trampling, differences in physical soil conditions can be observed. At a high trampling intensity, the density of the soil increases which results in a high mechanical impedance and in a low pore volume value. Differences in soil characteristics have been observed for example between the soil
Table 5. Soil data for plots in the “Westduinen” in which two types of *Plantago lanceolata* have been observed (values based on 26 measurements)

<table>
<thead>
<tr>
<th>Type</th>
<th>Organic matter (%)</th>
<th>Soil moisture (% by dry weight)</th>
<th>Pore volume (%)</th>
<th>Water-filled pores (%)</th>
<th>Air-filled pores (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Type 1</td>
<td></td>
<td>12.0</td>
<td>48.9</td>
<td>68.7</td>
<td>10.4</td>
</tr>
<tr>
<td></td>
<td>95% confidence interval</td>
<td>10.8–13.2</td>
<td>39.7–58.0</td>
<td>64.5–72.8</td>
<td>7.5–13.3</td>
</tr>
<tr>
<td>Type 2</td>
<td></td>
<td>6.8</td>
<td>21.2</td>
<td>63.3</td>
<td>3.8</td>
</tr>
<tr>
<td></td>
<td>95% confidence interval</td>
<td>6.0–7.6</td>
<td>15.7–26.7</td>
<td>60.5–66.0</td>
<td>2.7–4.9</td>
</tr>
<tr>
<td></td>
<td><strong>statistical differences between type 1 and 2</strong></td>
<td><strong>significant</strong> (p&lt;0.002)</td>
<td><strong>significant</strong> (p&lt;0.002)</td>
<td><strong>not significant</strong> (0.05&lt;p&lt;0.1)</td>
<td><strong>significant</strong> (p&lt;0.002)</td>
</tr>
</tbody>
</table>
Table 6. Related soil characteristics determined in a transect perpendicular to a heavily trampled cattle path in the dune grassland “Westduinen” (see also Fig. 1)

<table>
<thead>
<tr>
<th></th>
<th>Soil resistance (kg/cm²)</th>
<th>Pore volume (%)</th>
<th>Soil moisture (% by dry weight)</th>
<th>Organic matter (% loss of ignition)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5 cm</td>
<td>10 cm</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>¯x  S.E.</td>
<td>¯x  S.E.</td>
<td>¯x  S.E.</td>
<td>¯x  S.E.</td>
</tr>
<tr>
<td>A  (south-west facing slope)</td>
<td>15.0  0.6</td>
<td>17.9  0.7</td>
<td>57.5  0.5</td>
<td>15.5  3.8</td>
</tr>
<tr>
<td>B₁ (path edge)</td>
<td>23.1  0.7</td>
<td>20.6  0.9</td>
<td>62.9  1.9</td>
<td>35.1  4.6</td>
</tr>
<tr>
<td>B₂ (cattle path)</td>
<td>26.2  0.7</td>
<td>32.2  1.0</td>
<td>52.7  2.7</td>
<td>17.9  2.2</td>
</tr>
<tr>
<td>B₃ (path edge)</td>
<td>19.6  0.8</td>
<td>17.4  1.7</td>
<td>63.7  1.4</td>
<td>34.7  3.0</td>
</tr>
<tr>
<td>C  (north-east facing slope)</td>
<td>19.9  0.8</td>
<td>11.8  0.5</td>
<td>58.0  1.1</td>
<td>14.0  0.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
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of coenon 8 (heavily trampled) and that of coenon 5 (scarcely trampled) on the "Heveringen" (Table 4c). High densities may limit soil aeration conditions for the growth of plants (Gill & Miller 1956; Warnaars & Eavis 1972) and, in the case of sandy soils, increase the water availability (Liddle & Greig-Smith 1975a; Krüger 1970; Rao et al. 1973). The damage to the vegetation by intense trampling may result in an open vegetation layer which, in the long term, leads to a low organic matter content. Under certain conditions very high trampling intensities result either in bare, loose soils (Van der Werf 1970) or in a very compacted subsoil in which the water permeability has been inhibited (Table 6; B₂). The high values of pore volume as found in the soils of the intensely trampled areas of the hygro- and mesosere of the "Westduinen" (Table 4a) must be ascribed to the fact that the roots occur for the greater part in the upper 10 cm of the soil layer. The mechanical activity of a dense root system loosens the soil, which effect was also observed by Hettiaratchi & Ferguson (1973).

The reduced length of the roots in these soils is caused partly by the high water table (cf. Brouwer 1978) and partly by the compacted subsoil (Kramer 1969; Schuurman 1971; Kar et al. 1976). Furthermore, due to a relatively high organic matter content (Table 4a) pore volumes are higher as compared with sandy soils poor in organic matter (Schothorst 1968). The low values in pore volume as found on path B₂ (Table 6) are caused by the low content in organic matter as well as by the absence of many roots in this bare soil. As shown in Table 6, and, for example, in Table 4c, coena 3b and 6, the pore volumes of the soil of slopes are also low, which is probably caused by the fact that at the foot of a slope small soil particles washed down from the top and fill up the large pores. Penetrometer measurements are apparently not sufficiently accurate to determine these differences in soil compaction. Another difficulty in the measurement of soil resistance in the field with a penetrometer is the occurrence of a dense root layer, which can give less accurate results. The use of a penetrometer under experimental conditions appeared to be less problematical (Blom 1977). To replace the penetrometer other apparatuses have been developed (Cockroft et al. 1969; Baligar et al. 1975); these are, however, unpractical for field use.

It can be stated that small differences in values of soil resistance are considerably less important than small differences in values of pore volume. Probably due to the trampling by cattle on the "Westduinen", the soil resistance at a depth of 10 cm is in general considerably higher than that at 5 cm (Table 4a, b). The forces applied to the soil by walkers are much smaller; at the "Heveringen" smaller differences between the values in soil resistance between 5 and 10 cm were observed (Table 4c).

The occurrence of the Plantago species in the areas studied corresponds well with the results obtained in the experiments under controlled conditions (Blom 1976, 1977, 1978a, b). The observation in the field that P. major ssp. major and P. coronopus are more able to grow on compacted
sandy soils than *P. lanceolata* can be explained by the fact that the primary
roots of the first mentioned taxa are able to penetrate compacted soil
layers very quickly (Blom 1976, 1978a). Furthermore, the growth of *P.
major* is stimulated by the higher water availability in compacted sandy
soils (Blom 1976). The presence of *P. major* ssp. *major* on paths can be
explained by the fact that the seedlings as well as the full-grown plants
of this species are very resistant to trampling (Blom 1977, 1978b). It has
also been demonstrated (Blom 1977) that the growth of *P. major* ssp. *major*
is limited by the effects of other plants. Furthermore, the root competition
factor appears to be very important (Blom 1979). In the field *P. major*
ssp. *major* occurs on more open sites than the other species under study;
*P. lanceolata* especially is able to establish in dense vegetation layers.
In Blom (1977) it has been explained already that, in spite of the vulner­
ability to trampling of the seedlings of *P. coronopus*, this species is able
to establish on trampled sites.

It can be concluded that large-scale synecological investigations as
presented in this paper combined with studies under controlled conditions
will give a good idea of the behaviour of species and their communities
in the field. More detailed information on the behaviour of particular in­
dividuals or populations of plant species over a longer period, can be
obtained by demographic investigations supplied with genetical, physio­
logical, microbiological and soil studies. For such detailed studies, in­
vestigations on the phytosociological level will be a valuable starting point.

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