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

I. Soil compaction, soil moisture and seedling emergence

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SUMMARY

The mechanical resistance of coastal dune sands was found to be an important factor for the emergence and seedling establishment of Plantago lanceolata, P. coronopus, P. major, P. media, and Potentilla tabernaemontani.

Under optimal soil-moisture conditions, emergence and establishment of all species occur in higher percentages on the loose sandy soils than on the compacted substrates; the radicles of P. major and P. coronopus are more capable of penetrating compacted sandy soils than those of the other species under study.

Under low soil-moisture conditions, the highest numbers of seedlings of the Plantago species are found on the compacted soils; in contrast, Potentilla is found most frequently on the loose soils. Under these conditions the emergence of Plantago species is limited more by the low water supply than by the high mechanical resistance of the soil. The emergence of P. major and P. media is more susceptible to adverse moisture conditions than that of the other species.

In experimental plots in the field, P. major and P. media are the best adapted to the conditions found in compacted sandy soils, whereas the occurrence of seedlings of the other Plantago species is favoured on the loose, relatively dry soils.

RÉSUMÉ

La résistance mécanique du sable des dunes côtières s’est avérée être un facteur important pour la levée et l’établissement de plantules de Plantago lanceolata, P. coronopus, P. major, P. media et Potentilla tabernaemontani.

Sous des conditions optimales d’humidité, la levée et l’établissement des plantules est plus précoce, avec des pourcentages plus élevés sur sol sableux meuble que sur substrat compact; les radicules de P. major et P. coronopus pénètrent plus facilement les sols sableux compacts que les autres espèces étudiées.

Sous une faible humidité, il y a davantage de plantules de Plantago sur sol compact, alors que Potentilla se rencontre plus fréquemment sur sol meuble. Dans ces conditions, l’apparition de Plantago dépend plus de la faible quantité d’eau disponible, que de la haute résistance mécanique du sol. L’apparition des plantules de P. major et P. media est plus sensible aux conditions défavorables d’humidité que les autres espèces.

Les résultats expérimentaux sur des parcelles in situ montrent que P. major et P. media sont le mieux adaptées aux sols sableux compacts tandis que les autres espèces de Plantago sont favorisées par des sols meubles relativement secs.

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I. INTRODUCTION

One of the subjects of the ecological research program for the coastal dune areas in The Netherlands concerns the influence of recreation and grazing on the vegetation. Both involve trampling of the vegetation, which also leads to compaction of the soil.

The aim of the present investigation was to determine the effects of trampling and soil compaction on the development of the semi-natural dune vegetation and on the occurrence of some Plantago species. These species were chosen because trampling and soil compaction are thought to be of importance for their distribution (Bates, 1935, Westhoff and Van Leeuwen, 1966, Westhoff, 1967, Goldsmith et al, 1970 and Burden and Randerson, 1972). Of the five species under study, Plantago lanceolata L., P. coronopus L., and P. major L. are found on dune soils compacted and trodden to various degrees. For comparison of these dune species with a species originating from moderately trodden loam or clay soils, P. media L. was selected. Potentilla tabernaemontani Aschrs., which grows in the dune area mainly on very lightly trodden soils, was also included to compare the behaviour of the Plantago species with that of a species belonging to a different genus.

For the investigation of the occurrence of plant species under various experimental conditions, a division must be made between the effects of these conditions on the germination, emergence, and development of the seedlings on the one hand and on the other stages of the life cycle of the plant, on the other. In this first paper of the forthcoming series the results of sowing experiments on bare dune soils differing in compaction and moisture are discussed. The effects of compaction and moisture on radicle emergence (the first clear manifestation that germination has taken place) and on the emergence and establishment of seedlings were studied separately and in combination. These experiments were performed in a growth cabinet under fixed conditions as well as in experimental plots in the field. In the experiments done in the growth cabinet a distinction was made between surface-lying and buried seeds, because both situations occur under field conditions, particularly on paths. On a path the chance is very high that seeds lying on the soil surface will be pressed into the soil by trampling. Furthermore, many authors have reported that the planting depth is an important factor for seed germination (Taylor, 1962, Taylor et al., 1966, Onyekwelu, 1972). Together with soil compaction and soil moisture, the factor of trampling was studied in relation to the emergence and establishment of Plantago seedlings in greenhouse experiments and in sowing experiments under field conditions. The results of the trampling experiments will be reported in the second paper of this series.

Studies on the influence of soil compaction on the emergence of seedlings are found mainly in the agricultural literature. Most of the authors found a depressed emergence of seedlings at increasing degrees of soil compaction. Richards (1953)
SOIL COMPACTION AND SEEDLING EMERGENCE

showed a decrease in emergence of bean seedlings with increasing hardness of the soil crust, and PARKER and TAYLOR (1965) and TAYLOR et al. (1966) reported that in laboratory studies emergence percentages of mainly gramineous seedlings decreased slightly as the soil compaction increased; in strongly compacted soils no emergence occurred. HANKS and THORP (1956) showed that an increase of bulk density of silty clay loam, silty loam, and fine sandy loam at field capacity resulted in a decrease of wheat seedling emergence. BARLEY and GREACEN (1967) described experiments in which it was demonstrated that mechanical resistance in general can exert a negative influence on seedling emergence.

In ecological research, soil compaction is considered to be an important ecological factor (VAN LEEUWEN, 1966, VAN DER MAAREL, 1966 a, 1966 b). Besides the effect of walking by people and animals and the influence of vehicles (VAN DER WERF, 1970, LIDDLE, 1975, LIDDLE and GREIG-SMITH, 1975 a, b), fluctuation of the groundwater level and the impact of raindrops on soils can change the compaction of surface layers (McINTYRE, 1955, 1958). HARPER et al. (1965) observed that modification of soil microtopography by compaction causes a reduction in the establishment of some plant species. According to SHELDON (1974), the mortality of surface-lying seeds of some Compositae increased with compaction. PEMADASA and LOVELL (1974), who studied the establishment of seedlings of some dune annuals planted in compacted soils, attributed the high mortality of the planted species mainly to the competition of the perennial vegetation and the high mechanical resistance of the wet soil.

II. MATERIALS AND METHODS

(a) Growth-cabinet experiments

The experiments on the radicle and seedling emergence of the four Plantago and one Potentilla species were performed in a growth cabinet under fixed climatological conditions, i.e., 18 hours light, 6 hours darkness, temperature 24°C, and relative air humidity 70 %. These experiments were carried out with seeds of Plantago lanceolata, P. coronopus, P. major, and Potentilla tabernaemontani, all collected on a grassland in the dune area of Voorne (The Netherlands), and with seeds of P. media from a limestone grassland in the southern part of The Netherlands (province of Zuid-Limburg). The seeds were stored in envelopes at room temperature for 2 years. In all of the experiments two hundred seeds of each species were sown separately in wooden boxes (30 × 30 × 10 cm.) filled with a dune sand poor in nutrients (humus content 0.5 %, pH 9.0). Three series of boxes were prepared: in series A the soil was not compacted, in series C there was maximal compaction, and in series B the compaction was intermediate between A and C. Compaction of the soil was produced according to MURTY (1964) and ROSENBERG (1964), by ramming down the substrate in layers with a thickness of 3 cm.; after the packing of each layer, the soil surface was scraped to ensure a homogeneous soil profile.

Soil compaction was determined by measurement of the soil resistance with a penetrometer. The soil resistance in the upper 2 cm. was less than 0.1 kg/cm² in series A,
5 kg/cm² in series B, and 10 kg/cm² in series C. These soil-resistance values correspond with pore volumes of 45, 42, and 39 per cent, respectively. The latter values were determined at the end of the experiment and correspond reasonably well with those given by Schothorst (1968) for loose, medium compact, and compact, slightly humic sandy soils.

In two separate experiments a difference in soil-moisture levels was maintained. In the first experiment the percentage volume of water used for the three series was 21 (i.e., in all the series the amount of water was the same). Since the volumes of the substrates (sand + water) were identical in each box, the percentages weight of soil moisture were the highest in series A (18%) and lowest in series C (14%). In preliminary experiments these moisture levels were found to be adequate for optimal germination. During the experiment, evaporated water was replenished every 24 hours.

In this first experiment a distinction was made between surface-lying and buried seeds. The buried seeds were covered with a 3 mm. thick layer of dune sand with the same degree of compaction as the underlying soil layer. In the experiments with surface-lying seeds, the seeds of P. lanceolata, P. major, and P. media were lightly pressed into the soil surface to achieve sufficient seed-soil contact. This treatment was necessary because the relatively large seeds of these species on the soil surface would otherwise have failed to germinate. The seeds of P. coronopus are much smaller and seed-soil contact is always adequate.

As a control for germination in the series with buried seeds, seeds were placed on wet filter paper in Petri dishes and held in the dark in the growth cabinet. To check germination in the series with surface-lying seeds, the same regime of 16 hours of light and 8 hours of darkness at a temperature of 24°C was applied to seeds in Petri dishes.

Thus the first experiment was performed with five plant species, at three levels of soil compaction with buried and with surface-lying seeds.

In the second experiment a much lower moisture level was applied; the initial value for soil water was 7.8 per cent volume (identical quantities of water in all boxes). This experiment with buried seeds was carried out in the same way as the first experiment. After emergence had reached a constant level, the soil moisture was brought to 9.2%. For P. major, P. media, and Potentilla tabernaemontani the moisture level was later raised to 10.4% and for the first two of these species subsequently to 11.7%. Finally, the water content was raised for all species to the optimal of 21 per cent volume.

All of the experiments were carried out in triplicate, and differences between groups of replicates were tested with the X² test of independence or Fisher’s exact test.

(b) Experiments in open plots under field conditions

These experiments were carried out in an experimental garden in the dune area of Voorne. The original humic soil was removed, leaving a groove with a depth of 1 m., a width of 3 m., and a length of 18 m. The groove was divided into six compartments, each measuring 9 sq.m. The compartments were separated by concrete walls. Each compartment was filled with the same dune sand as was used in the growth-cabinet experiments described above. Plastic foil was attached to the sides of the groove to prevent contact between the original humic soil and the dune sand.

Compaction of the soil was achieved by ramming down the substrate in layers of 20 cm.; after packing, the surface of each subsoil was scraped to give a homogeneous soil profile. Two of the compartments were filled with loose dune sand; in a second pair the soil was brought to maximal compaction (penetrometer value: 10 kg/cm² on a depth of 2 cm.); in the remaining two compartments the resistance of the soil 2 cm. beneath surface was 5 kg/cm². In this way two plots could be compared with series A, two with series B, and
two with series C in the growth-cabinet experiments. The ground-water level in the plots was about 70 cm. below the soil surface, and soil humidity in the top layers depended on natural rainfall. In each plot 2 x 100 seeds each of *P. major*, *P. lanceolata*, *P. coronopus*, and *P. media* were sown separately in August 1972; in this way four replicates per species could be distinguished. The seeds were covered with 3 mm. of dune sand which was given the same degree of compaction as the underlying layer. During the experiment the emergence and establishment of seedlings were investigated. The penetrometer values were determined just before sowing and at the end of the experiment.

### III. RESULTS

(a) **Growth-cabinet experiments with buried Plantago seeds at an optimal moisture level**

In this experiment the emergence of the *Plantago* seedlings from seeds buried in loose (A), moderately compacted (B) and compacted dune soils (C) at optimal soil humidity was determined. Seedlings were considered to have emerged when the cotyledons appeared above the ground. As can be seen in Figure 1 a-d, the emergence of all studied *Plantago* seedlings occurred sooner and in higher numbers on the loose dune soils (mechanical resistance 2 cm. below the surface <0.1 kg/cm²) than in the other series. The lowest percentages of emerged seedlings were found either on the soils with the highest degree of compaction (10 kg/cm²) or on the moderately compacted soils (5 kg/cm²). At the end of this experiment the differences in total numbers of emerged *P. lanceolata* seedlings between series A and C were significant (*p*<0.05). For *P. lanceolata* in particular, the rate of emergence of seedlings on the compacted soils was slower during this experiment than in the other series. The differences between the series with the highest and lowest numbers of *P. major* and *P. media* seedlings were also significant (*p*<0.05).

Germination of the seeds of *P. major* proved to be season-dependent: in the winter under laboratory conditions seeds of this species showed a lower percentage of germination, which was also reported by Salisbury (1965) and Groot (1973). These authors found germination of this species to be associated with temperature changes and, in general, the dormancy decreases after storage of the seeds for more than 2 years. Figure 1 c shows the mean results of tests carried out in summer (s) and winter (w).

(b) **Growth-cabinet experiments with buried Plantago seeds at a low moisture level**

The results of this experiment are given in Figure 2 a-d. These graphs clearly show that, in contrast with the experiment at an optimal moisture level, all *Plantago* species emerged sooner and with higher percentages on the compacted than on the loose soils. The appearance of the first seedlings of *P. major* occurred about 5 days earlier on the compacted than on the moderately compacted soils and even
10 days earlier than on the loose substrates. *P. media* emerged about 5 days earlier on the compacted soils than on the others. The differences in emergence of the first seedlings of *P. lanceolata* and *P. coronopus* between the soils differing in compaction were smaller. After 20 days seedling emergence reached a constant level, and at this time the soil-moisture level was raised to 9.2 per cent volume.

![Graphs](image)

Fig. 1. — The influence of soil compaction at an optimal soil-moisture level on seedling emergence from buried seeds of four *Plantago* species (mean values of three replicates).

For *P. major* the results of experiments carried out in the summer (s) and the winter (w) are given separately.

- • loose soil; penetrometer value < 0.1 kg/cm²;
- + moderately compacted soil; penetrometer value 5 kg/cm²;
- ○ compacted soil; penetrometer value 10 kg/cm²;
- ▲ control.

This increase resulted in the emergence of more *P. lanceolata* and *P. coronopus* seedlings, but the relative differences between the various series remained. The emergence of *P. major* and *P. media* was less affected by this increase in the soil humidity. The graphs in Figure 2 c-d show that raising of the soil humidity to 10.4% resulted in the appearance of more seedlings of *P. media* and *P. major*. After 40 days and at 11.7% soil moisture, the differences between the series persisted. At the
end of this experiment the differences between series A and C were significant for *P. lanceolata* and *P. coronopus* (*p* < 0.005) and between series B and C for *P. major* and *P. media* (*p* < 0.05).

The relatively low percentages of emerged seedlings of *P. major* and *P. media* are probably due to the fact that during this experiment the low soil humidity resulted in premature death of the seeds of these species. When the water content was raised to the optimal level (21 vol. %) at the end of the experiment, the results show that most of the still ungerminated seeds of *P. lanceolata* and *P. coronopus* had emerged, whereas the other species showed no additional emergence.
Fig. 3. — The influence of soil compaction at an optimal soil-moisture level on radicle emergence and seedling establishment from surface-lying seeds of four Plantago species (mean values of three replicates). Solid lines indicate percentages of established seedlings, dashed lines the percentages of radicle emergence.

- ● loose soil;
- + moderately compacted soil;
- ○ compacted soil;
- ▲ control.

It should be noted that the experiment was started at a soil moisture content of 7.8%; below this level, no germination of *P. major* and *P. media* took place. In contrast, *P. lanceolata* and *P. coronopus* were able to germinate at a lower moisture level (about 6.0 vol.%).

(c) Growth-cabinet experiments with surface-lying seeds at optimal soil humidity

The results of this experiment are presented in Figure 3 *a-d*, which gives the percentages of both germinated seeds and established seedlings. The seeds were considered to have germinated when the radicle emerged from the covering structures of the seed. Following Heydecker (1972), this stage is called radicle emergence.
The time at which the radicle grew into the substrate and the cotyledons became visible was taken as the moment of establishment. In the case of *P. coronopus* (Fig. 3b) it was impossible to distinguish between radicle emergence and seedling establishment because the radicle grew into the substrate immediately after germination. For all species, the highest percentages of germinated seeds and of seedling establishment were found on the loose soil; the lowest percentages occurred significantly on the most compacted substrate. There was, however, considerable difference between the four *Plantago* species.

After sowing of *P. lanceolata* at least ten days were required for the emergence of the radicle. The first seedlings of this species became established on the loose soils 2 days after the appearance of germinated seeds; on the moderately compacted soils this period came to 4 days and on the compacted soils to 6 days. On loose soil, 93% of the germinated seeds had reached the stage of established seedling at the end of the test; on moderately compacted and compacted soils these values were only 50 and 42%, respectively.

For *P. coronopus*, it was found that the first seedlings appeared after 11 days. The time between sowing and the appearance of the first germinated seeds of *P. major* came to 2 or 3 days on all substrates. The seedlings established themselves rapidly in all series, 2 or 3 days being required for this process. On the loose and moderately compacted soils, all germinated seeds developed into established seedlings; on the compacted soil this percentage was still 89.

For *P. media*, 7 days were required before the first emergence of the radicle was observed on the loose soil; on the moderately compacted soil this time was 9 days and on the compacted soil 11 days. On the loose soils the first seedlings became established 9 days after sowing and on the moderately and compacted soils 12 and 15 days, respectively. During this experiment the percentages of germinated *P. media* seeds reaching the stage of established seedlings were 84, 62, and 51 on the loose, moderately compacted, and compacted soils, respectively.

For surface-lying seeds of all species, the differences found at the end of the test between the highest and lowest levels of established seedlings were significant (*P. coronopus* and *P. major* *p*<0.01; *P. lanceolata* and *P. media* *p*<0.005).

(d) Experiments with buried and surface-lying seeds of *Potentilla tabernaemontani*

The results obtained with buried seeds of *Potentilla tabernaemontani* at an optimal soil-moisture level are given in Figure 4a. These graphs show that the emergence percentages of buried seeds on loose dune soils differ significantly (*p*<0.01) from those on the compacted soils. The rate of emergence was also higher on the loose soils than on the compacted soils.

The results of the experiments with seeds buried at a low soil-humidity level are given in Figure 4b. As for the *Plantago* series, the experiment was started at a soil humidity of 7.8 per cent volume. When seedling emergence reached a cons-
tant level, the soil humidity was increased to 9.2%. This level was maintained from 16 to 22 days after sowing; a subsequent increase of the moisture level resulted in the appearance of more seedlings. In contrast to similar experiments with Plantago

![Diagram](attachment:figure4.png)

*Fig. 4. — The influence of soil compaction and soil humidity on seedling emergence, radicle emergence and seedling establishment of *Potentilla tabernaemontani* (mean values of three replicates). (a) buried seeds at an optimal soil-moisture level; (b) buried seeds at a low soil-moisture level; (c) surface-lying seeds at an optimal soil-moisture level. In (a) and (b) the solid lines indicate the percentages of emerged seedlings; in (c) the solid lines indicate the percentages of established seedlings and the dashed lines the percentages of radicle emergence.

- ○ loose soil;
- + moderately compacted soil;
- O compacted soil;
- ▲ control.

seeds, *Potentilla* emerged sooner on the loose soil than on the moderately compacted and compacted substrates. At the end of the experimental period the differences between the total numbers of *Potentilla* seedlings on the loose and the compact soils were significant (*p* < 0.05).
The results of the tests with surface-lying seeds at optimal soil moisture are given in Figure 4c, which shows the radicle emergence and the establishment of the seedlings. As for *Plantago, Potentilla* seeds lying on loose soils performed better than the seeds lying on compacted or moderately compacted substrates. The interval before the first radicles emerged on the various compacted soils was comparable with that found for *P. lanceolata*. The interval between radicle emergence and establishment of the seedlings on the loose soils was approximately 2 days, on moderately compacted and compacted soils it took longer: 3 and 6 days, respectively. During this experiment the percentages of germinated seeds reaching the stage of established seedlings were about 91, 87, and 60 for the loose, moderately

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**Fig. 5.** — The influence of soil compaction on seedling emergence from buried *Plantago* seeds in experimental plots in the field (mean values of four comparable plots). For the columns on the right a distinction was made between newly emerged plants and plants of the preceding year, the upper part representing the former and the lower part the latter. The vertical bars represent twice the standard deviation.

- loose soil;
- moderately compacted soil;
- compacted soil.
compacted, and compacted soils, respectively. At the end of the experimental period the difference between established seedlings on the loose and compacted substrates was significant ($p < 0.01$).

(e) Experiments in open plots under field conditions

The results of the emergence of Plantago species sown in the experimental field plots are given in Figure 5 a-d. Graphs a and b show percentages of emerged seedlings of *P. lanceolata* and *P. coronopus* in 1972 and 1973. Since no seedlings of *P. major* and *P. media* emerged in 1972, graphs c and d show the percentages of emergence in 1973 and 1974.

![Penetrometer values at depths of: • 2 cm; x 5 cm; ▲ 10 cm.](Image)

- Fig. 6. — Penetrometer values, measured at three depths in the field plots just before sowing (August 1972) and at the end of the experiment (September 1974). The vertical bars represent twice the standard deviation. A = loose soil; B = moderately compacted soil; C = compacted soil.

Four days after sowing, 20% of the planted seeds of *P. lanceolata* and about 15% of *P. coronopus* had emerged on the plots with the loose soil. On the moderately compacted soil only emergence of *P. lanceolata* (9%) was obtained in this time. On the compacted soil, on average 15% of *P. lanceolata* and 5% of *P. coronopus* had emerged at that time. Six days later, the emergence of *P. lanceolata* and *P. coronopus* on all plots reached a level which remained more or less constant until the end of October 1972. In 1972 the highest percentages of *P. lanceolata* and *P. coronopus* seedlings occurred on the loose soil and the lowest percentages were found on the moderately compacted substrate. The 1973 results are also shown in Figure 5 a and b, where a distinction is made between plants present since 1972 and seedlings originating from seeds sown in 1972 and emerged in 1973. For *P. lanceolata* and *P. coronopus*, the differences in total numbers of living plants between the various plots were approximately the same in 1973. This was probably due to the decreasing compaction in the upper layers of the moderately compacted and compacted soils.

In 1973 and 1974 significantly more seedlings of *P. major* and *P. media* occurred on the compacted than on the loose substrates (Fig. 5, c and d). Initially, *P. major*
occurred in very small numbers on the loose soil; at the end of 1973, this species disappeared completely from this substrate and at the end of 1974, *P. major* was only present on the compacted soil. On all plots the total number of *P. media* seedlings was higher than that of *P. major*.

The soil humidity in the experimental plots varied widely (mean value about 5 per cent volume in the upper layers), and germination generally occurred after a spell of rainy days.

Penetrometer measurements were made twice: just before sowing and in September of 1974. These measurements (Fig. 6 a-b) were made at depths of 2, 5 and 10 cm. at similar soil-moisture levels in 1972 and 1974. At a depth of 2 cm. the differences between the various plots were nullified in 1974, whereas in all series the mechanical resistance at 5 cm. was increased. At a depth of 10 cm. the original degree of compaction still existed except in the plots with the loose substrates, in which a slight degree of compaction had occurred.

IV. DISCUSSION

Factors closely related to soil compaction are the mechanical resistance, availability of moisture, aeration and the temperature of the soil (Eavis, 1972; Scott Russell and Goss, 1974; Liddle and Moore, 1974). Shifts in these factors are due to changes in total pore volume (bulk density) and in pore size distribution. In the present study, mechanical resistance, total pore volume and soil humidity were considered as most important for the emergence of seedlings. The other factors were not studied separately because the size distribution of the sand particles lay within a small range and the seeds were planted on the surface or were covered with only a thin layer of sand.

The growth-cabinet experiments at optimal soil-moisture level showed the highest percentages of emerged seedlings of all five species on the loose soils (Figs. 1, 3, 4 a, and 4 c). The lower percentages of emerged seedlings on the compacted soils can be ascribed either to poorer germination of the buried seeds or to the death of germinated seeds before the cotyledons appeared above ground. For the present experiments the rate of gas exchange will not be limiting for germination and it is likely that the high mechanical resistance in compacted soils was responsible for the premature death. This was also reported by Arndt (1965) for pea seedlings. For surface-lying seeds the unfavourable effect of soil compaction was still more pronounced; the differences in total numbers of seedlings between loose and compacted soils were higher than for buried seeds. The higher percentages of germinated seeds on the loose soils are probably due to roughness of the surfaces of these substrates; particularly on the loose soils, daily watering caused an increase of the heterogeneity of the surface. Harper et al. (1965) and Dowling et al. (1971) reported that on a rough surface, some seeds will lie on more suitable sites than others. The longest intervals between radicle emergence and establishment were
found for *P. lanceolata*, *P. media* and *Potentilla tabernaemontani*; the roots of *P. major* and *P. coronopus* are more capable of penetrating compacted soils. On compacted sandy soils germination and establishment of surface-lying seeds of *P. major* occurred sooner and in higher percentages than was the case for the other species. Only 2 days were required for the radicle emergence of *P. major*, and after 20 days on compacted soil 89% of the germinated seeds had developed into established seedlings. In contrast, more than 10 days were required for the radicle emergence of *P. lanceolata* and after 50 days on compacted soil only 42% had become established seedlings. The results of the experiments with surface-lying seeds show clearly that during the first stages of the life cycle, *P. major* is better adapted to compacted soils than any of the other species studied.

The growth-cabinet experiments with buried seeds at low soil-moisture levels showed that the emergence rate and the maximal percentages of emerged seedlings were lower in these experiments than under optimal moisture conditions. Furthermore, in spite of the higher mechanical resistance of the soil in the compacted series the emergence percentages of the *Plantago* species were higher on these soils than on the loose substrates (Fig. 2). These findings indicate that at low soil-moisture levels the small quantity of water is more important as a limiting factor for germination and emergence than the mechanical resistance. Like the highest percentages of emerged seedlings, the shortest interval between sowing and the emergence of the first seedlings was found on the compacted soils. These results must be ascribed to the better moisture supply to the seeds in compacted soils; the capillary rise being better in compacted sandy soils than in loose sandy substrates. Liddle and Greig-Smith (1975 a) suggested that under dry conditions the growth of plants may be enhanced by greater availability of water in a compacted sandy soil. It is remarkable that in the low soil humidity experiments the most *Potentilla tabernaemontani* seedlings were found in loose soils. For the emergence of *Potentilla* seedlings, a low moisture level is apparently less limiting than mechanical resistance of the soil.

The differences in behaviour in the experimental plots in the field between *P. lanceolata* and *P. coronopus* on the one hand and *P. major* and *P. media* on the other were probably caused by the combined action of the factors of mechanical soil resistance and soil humidity. The soil humidity of these barren sand plots was, in general, very low. Because *P. lanceolata* and *P. coronopus* germinated better than *P. major* and *P. media* at low levels of soil humidity, it may be supposed that for the latter, also under these conditions, soil humidity is more limiting for germination than is the case for the former species. This conclusion is supported by the observation that the emergence of *P. major* and *P. media* was higher on the compacted than on loose soils because the water availability is greater on compacted soils. The results obtained in the experimental plots show that the mechanical resistance was the most important unfavourable factor for the emergence of *P. lanceolata*.
SOIL COMPACTION AND SEEDLING EMERGENCE

and P. coronopus. The low levels of emerged seedlings on the moderately compacted soils are possibly due to the combination of two unfavourable factors, namely a certain degree of soil resistance and a relatively low water availability.

In conclusion, it can be stated that with respect to seedling emergence and establishment on soils with a high mechanical resistance P. major is best adapted, followed by P. media; P. lanceolata being the least well adapted. P. coronopus seems to be more or less indifferent to mechanical resistance. P. major is very effective in penetrating compacted soils: the establishment of its seedlings from surface-lying seeds was better than that of any of the other species. The emergence of P. major and P. media is very susceptible with respect to adverse moisture conditions. This may explain the absence of these species in loose but dry sandy soils; P. coronopus and P. lanceolata are better adapted to these soil conditions.

The trials with buried seeds of Potentilla tabernaemontani showed that the emergence of the seedlings of this species is more limited by soil compaction than that of the Plantago species. For surface-lying seeds, this species appears to be more capable of soil penetration than P. lanceolata but less so than the other Plantago species.

Most of the present results are in accordance with the occurrence of these species in nature. In sand dunes P. lanceolata is found mainly on grassy, dry or humid places with a loose or moderately compacted soil (i.e., dune grasslands). P. major occurs mainly in open habitats on humic, humid, and compacted soils (i.e., paths). The typical coastal dune species, P. coronopus, is found on loose as well as on compacted soils (i.e., open sandy soils and paths). P. media occurs mainly in grassy places on moderately compacted limestone, loam, or clay soils (i.e., verges in grasslands). In the dunes Potentilla tabernaemontani is found mainly on sunny slopes of dry, basic grasslands with a loose or moderately compacted soil.

The synecological significance of the same species in relation to trampling and soil compaction will be discussed in a forthcoming paper.

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