

## GERMINATION, SEEDLING EMERGENCE AND ESTABLISHMENT OF SOME PLANTAGO SPECIES UNDER LABORATORY AND FIELD CONDITIONS\*

C. W. P. M. BLOM

Instituut voor Oecologisch Onderzoek, Afd. Duinonderzoek "Weevers' Duin" Duinzoom 20 A, 3233 EG Oostvoorne

### SUMMARY

(a) The germination of *Plantago lanceolata* L., *P. coronopus* L., *P. major* L. ssp. *major*, *P. major* L. ssp. *pleiosperma* Pilger, *P. media* L., and *P. maritima* L. in relation to the age of dry-stored seeds was investigated under laboratory conditions. In general, higher percentages of radicle emergence were found with two- to five-year-old seed than with fresh seed.

Only *P. lanceolata* and *P. media* seeds germinated in complete darkness. A feature of interest was the high germination of both subspecies of *P. major* in so-called green safelight.

(b) The germination and early establishment were tested on various microsites, obtained with glass beads of various sizes. At increasing particle size, an increase in radicle emergence was found for large seeds (*P. lanceolata* and *P. media*). Root penetration of the surface occurred sooner on substrates of large particles than on those of small ones.

The effects of size of the glass beads on germination and penetration were less in species with small seeds than in species with large seeds.

(c) Sowing tests in the field resulted in relatively high numbers of established *P. lanceolata* and *P. coronopus* seedlings in open and dry habitats. *P. lanceolata* seedlings were able to establish themselves in tall dense vegetation layers. *P. major* ssp. *major* occurred most frequently on moist and open sites with a compact soil. On trodden paths *P. major* and *P. coronopus* seedlings showed opposite mortality curves.

### 1. INTRODUCTION

Within the scope of a study on the effects of trampling and soil compaction on the behaviour of some *Plantago* species during the various stages of their life-cycle (BLOM 1976, 1977) a number of experiments was performed with the aim of analysing the germination capacity (the emergence of the radicle) and the emergence and establishment of seedlings under laboratory and field conditions. STEINBAUER & GRISBY (1957), SAGAR & HARPER (1960, 1964), SALISBURY (1965), GROOT (1973), and ARNOLD (1973) have already reported on germination of *Plantago* species. Most of these experiments were carried out with fresh seeds. Under natural conditions, however, the seedbank of a soil consists of seeds of different age. In the present paper (in 3.1.) an impression will be given of the influence of age of dry-stored seeds on the germination of *Plantago lanceolata* L.,

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*P. coronopus* L., *P. major* L. ssp. *major*, *P. major* L. ssp. *pleiosperma* Pilger, *P. media* L., and *P. maritima* L. Besides tests performed in light and complete darkness, experiments were carried out with seeds exposed to short periods of dim daylight. The ecological background for this approach is that, under certain conditions, seeds may be exposed to small quantities of daylight which can result in germination (WESSON & WAREING 1969a). Simultaneously a germination test in darkness was designed in which seeds were exposed temporarily to dim green light, since quite a number of described germination experiments are performed under such conditions.

In previous papers (BLOM 1976, 1977) some attention was paid to ecologically important differences between species in the stages of radicle emergence, seedling emergence, and seedling establishment. As shown by DOWLING et al. (1971) and by OOMES & ELBERSE (1976) the germination capacity depends on a sufficient contact between seed and soil water, which is influenced by the degree of soil compaction (BLOM 1976, and PATHAK et al. 1976). The availability of suitable microsites is also crucial for the process of seedling establishment (HARPER et al. 1965). The effects of various microsites on the radicle emergence and those of different particle sizes of the substrate on the early establishment of four *Plantago* species varying in the size of their seeds will be described in 3.2 of this paper.

In paper II of the series on trampling and soil compaction, a number of sowing experiments in the field were described; the final percentages of established seedlings as well as the percentages of seedlings which succumbed were given (BLOM 1977). However, the aspects of the establishment of seedlings during the course of the experiment have not been described. This aspect will be discussed in relation to the ecological significance in 3.3 of this paper.

## 2. MATERIALS AND METHODS

### 2.1 Laboratory germination tests

Seeds of *Plantago lanceolata*, *P. coronopus*, *P. major* ssp. *major*, and *P. major* ssp. *pleiosperma* were collected on the "Heveringen", a semi-natural grassland in the dune area of Voorne (The Netherlands). The first two species came from a dry site and both subspecies of *P. major* from a moist one. *P. maritima* seeds were collected on the "Kwade Hoek", a beach flat on the island of Goeree. *P. media* seeds came from a population occurring on a chalk grassland in the southern part of The Netherlands (Gerendal, province of Limburg). All seeds were stored in envelopes at room temperature. The germination tests were carried out in germination cabinets at temperatures of 15, 20 and 25°C as well as in the greenhouse (25 ± 4°C). A fluctuating temperature regime of 15–25°C (12 hours each) was also applied. The seeds which were placed on constantly wet filter paper in closed Petri-dishes, were considered to have germinated when the radicle emerged from the testa (radicle emergence). The effect of the age of the seeds on germination was investigated under light (photoperiod 18 h) and dark conditions. In tests in the dark a distinction was made between total darkness and two minutes of faint light a day. Furthermore, tests were performed in which seeds incubated in the dark

were exposed (two minutes a day) to green safelight. This light was obtained from a green monophosphor fluorescent tube (Philips TL40, colour 17), wrapped in a layer of blue "cinemoid" No. 62 and a layer of orange-yellow "cinemoid" No. 46. (Emission maximum at 520 nm, half-width 27.5 nm, estimated intensity at dish level  $0.7 \mu \text{W cm}^{-2}$ ).

## 2.2 Radicle emergence and early establishment on glass beads of varying size

These experiments were carried out with seeds of which the size decreased in the order *P. lanceolata*, *P. media*, *P. major* ssp. *major*, and *P. coronopus*. All seeds originated from sites described under section 2.1 and were stored in envelopes for three years at room temperature. The tests were performed in plastic boxes which were placed in a growth cabinet under a photoperiod of 18 hours at 24°C. Four series were prepared. Boxes were filled with round glass beads of a diameter varying between 0.01–0.05 mm (I), 0.17–0.25 mm (II), and of 0.89–1.23 mm (III). As a reference (IV) boxes were filled with dune sand (0.05–1.0 mm, median 0.19 mm). Before sowing, the dry substrates were brought to maximal density by means of a horizontal vibration at a high frequency. Each species was sown in five rows of ten seeds on the surface of each substrate; the experiments were carried out in triplicate. During the tests the soil-moisture content was maintained at 21 per cent by volume. To ensure a high humidity the boxes were covered with a plate of glass four centimetres above the surface. The final percentages of germinated seeds, of succumbed individuals and the length of the primary roots between seed-coat and point of penetration into the surface, or in case of dead individuals to the root tip, have been determined.

## 2.3 Establishment of seedlings in the field

In April 1974 a mixture of *P. lanceolata*, *P. coronopus*, *P. major* ssp. *major*, and *P. media* seeds were sown on fourteen plots (30 × 30 cm) on a dune grassland of Voorne. Two hundred seeds of each species were distributed uniformly over the plots. To study the course of the establishment of the seedlings during the growing season the location and performance of the individual plants were recorded on a map on scale 1:1 every fortnight from April until July and subsequently each month until October. For the plots not destroyed by rabbits the observations were continued in 1975. As this sowing experiment was carried out as part of a research project on the effects of trampling (BLOM 1977), the plots were chosen on the middle of paths (V), on edges of paths (M) and on loose soils (O).

Each fortnight the soil-moisture content in the upper 3 cm of the soil was determined. The soil-moisture level of the plots with the loose soil was very low (mainly between 4–10% by weight) and the vegetation layer low (0–5 cm) and open (cover 50%). The entire surface of the plots on the edges of paths was covered by a tall dense layer of vegetation mostly of herbs (10–15 cm) and the soil was moist ( $M_1, M_2$ : 13–27%;  $M_3$ – $M_5$ : 60–94%). The cover by vegetation of three of the plots on the paths ( $V_1$ – $V_3$ ) was between 70 and 85 per cent and the height of the plants did not exceed 7 cm. The other plots on the path were more open (cover

Table 1. Germination percentages\* under different light conditions in relation to the age of dry-stored seeds of six *Plantago* species. All results are obtained at 25°C, fourteen days after sowing. Most tests are performed with 10 × 50 seeds in each year.

Seed age in years	0**	1	2	3	4	5	6
<i>P. lanceolata</i>	a	10-55	52-76	76-86			
	b	22-59	86-94				
	c	—	57-75	76-100			
	d	—					
<i>P. coronopus</i>	a	32-97	84-91			65-92	
	b	31-67		66-98	24-57		14-27
	c	0					
	d	0					
<i>P. major</i> ssp. <i>major</i>	a	0-19	89-99			18-58	
	b	0	69-87			5-15	
	c	—	—	—	47-89		0-11
	d	0					
<i>P. major</i> ssp. <i>pleiosperma</i>	a	0-12	93-100		56-71		—
	b	0-7	64-100		0-36		—
	c	—	—	—	0-34		—
	d	0					
<i>P. media</i>	a	44-83	81-89				38-73
	b	5-36	75-86				22-69
	c	—	46-73				11-51
	d	—					
<i>P. maritima</i>	a	86-93					
	b	69-82					
	c	—	—	—	—	—	0-12
	d	—	—	—	—	—	
Seed age in years	0	1	2	3	4	5	6

\* The 95% confidence intervals are given (one interval for more years taken together means that no differences in germination were found)

\*\* Freshly collected seeds

a: Daily photoperiod 16 hours of light, 8 hours darkness

b: Complete darkness except for two minutes of faint daylight daily

c: Complete darkness except for two minutes of faint green light daily

d: Complete darkness

— insufficient observations available.

40–50%) and the vegetation was relatively low (2–3 cm). The soil-moisture levels found in plots V<sub>1</sub> to V<sub>5</sub> were below 50% by weight; the soil of plot V<sub>6</sub> was much wetter (93%). The characteristics of each plot have been given in more detail in a previous paper (BLOM 1977).

### 3. RESULTS

#### 3.1 Laboratory germination tests

The data of *table 1* show that the germination capacity of freshly collected seeds of most species was markedly lower than of older seeds. With the exception of *P. lanceolata*, all *Plantago* species studied germinated in lower numbers in the dark with daily two minutes of faint day- or green light than in the light. Only *P. lanceolata* and, to a lesser extent *P. media* were able to germinate in complete darkness. No radicle emergence in *P. coronopus* was observed in the dark or under green light conditions. The results obtained with both subspecies of *P. major* were of particular interest. In complete darkness no radicle emergence took place, whereas, especially for *P. major* ssp. *major*, under green light conditions considerable numbers of germinated seeds were observed. The results contradict those of HAWTHORN (1974) who still found some germination in complete darkness.

Temperature appeared to be an important factor for the germination of *P. media* and even more so for *P. major* ssp. *major*. The proportion of the seeds of these species capable of germination decreased strongly when the temperature fell below 20°C during incubation; the radicle emergence of fresh to three year old seed did not exceed 3 per cent; for older seeds this became 7 per cent. Below 18°C the radicle emergence of fresh *P. media* seeds was about 5 per cent, but older seeds came to a mean germination of 12 per cent. These results agree fairly well with those of SAGAR & HARPER (1960, 1964).

A fluctuating temperature regime (15–25°C) resulted in no more germinated seeds than a constant temperature of 25°C.

Although the germination-dormancy characteristics of seed stored under natural conditions can be different from results obtained with seeds stored under dry conditions at room temperature (HARRINGTON 1973), the data of the present study clearly show that only *P. lanceolata* and *P. media* seeds will be able to germinate reasonably well in the absence of light, which may occur in the field when the seeds are buried (cf. WESSON & WAREING 1969b). A short exposure to faint daylight of dark incubated seeds of *P. coronopus*, both subspecies of *P. major*, and *P. maritima* resulted in reasonable numbers of germinated seeds. The ecological relevance of such a phenomenon has already been discussed by WESSON & WAREING (1969a).

The observation in the field that the seedling emergence of *P. major* ssp. *major* and *P. media* occurred mostly in the late spring or summer can be explained by the fact that a relatively high mean temperature is necessary for the germination of those species.

### 3.2 Radicle emergence and early establishment on glass beads of varying size

As shown in table 2, the numbers of germinated seeds of *P. lanceolata* on the substrate with the smallest particles (I) were significantly lower than those on the other substrates ( $P < 0.01$  comparing I and II). An increase in germination at increasing particle sizes of the substrates was also found for *P. media*. In comparison with the other species on substrate I, lowest numbers of germinated seeds were found for *P. lanceolata* ( $P < 0.05$ ). The seeds second in size (*P. media*) germinated again in lower numbers on substrate I than those of *P. major* ssp. *major* ( $P < 0.05$ ). This increase in germination with decreasing seed size was also observed on substrate II.

Compared with the results on substrate I, the mortality of *P. lanceolata*, *P. media*, and *P. major* ssp. *major* was significantly lower on the glass beads of substrate II ( $P < 0.005$ ). At a decrease in seed size, a decrease in mortality of germinated seeds was found on each substrate; only on the largest beads (III) did all seedlings survive.

The sizes of the greater proportion of the sand grains are in the same range as those of the glass beads of substrate II. Only the germination of *P. lanceolata* on the sand soil was significantly (0.5% level) higher than on substrate II.

Death of seedlings was caused by the inability of the primary roots to penetrate a dense substrate surface. In particular *P. lanceolata* roots meandered over the surface to find a gap for penetration. This phenomenon was observed earlier (BLOM 1976) and also described for some other species by SHELDON (1974). When under the high humidity conditions no gap was found within about five days, the root-tips desiccated and became dark. Root penetration of all species followed almost immediately upon radicle emergence on the substrate with the large beads. The primary roots of *P. lanceolata* were able to penetrate the upper layer of substrate I relatively quickly. Penetration of the lower layers, however, appeared to be a difficulty which resulted in a high mortality of *P. lanceolata* seedlings (table 2). Compared with the other species the primary roots of *P. lanceolata* became obviously the longest on the surfaces of substrates I, II and on the sand soil (table 2). This species formed, especially on the sand soil, many laterals penetrating the surface, which, however, did not prevent a high mortality.

### 3.3 Establishment of seedlings in the field

Due to differences in trampling intensity, compaction and moisture content of the soil and height and cover of the vegetation layer, considerable differences in seedling establishment between the three groups of plots and sometimes between plots in one group were found. On the open sandy plots ( $O_1-O_3$ ) *P. lanceolata* and *P. coronopus* seedlings established themselves reasonably well and only a few individuals died (figs. 1a and 2a). From April to August, significantly more seedlings of *P. lanceolata* and less of *P. coronopus* were observed on plot  $O_2$ , i.e. the only plot with a vegetation layer (cover 50%), than on plots  $O_1$  and  $O_3$  ( $P < 0.05$ ). On the O-plots only 3 per cent of the *P. major* seeds had emerged; for *P. media* this percentage was still lower.

Table 2. Effects of substrates with different particle size on the radicle emergence, mortality and root length before penetration of four *Plantago* species.

Substrate Particle sizes (mm)	I 0.01-0.05			II 0.17-0.25			III 0.89-1.23			sand 0.05-1.0; median: 0.19		
	radicle emer- gence (%)	mortal- ity (%)	length** primary root (mm)	radicle emer- gence (%)	mortal- ity (%)	length primary root (mm)	radicle emer- gence (%)	mortal- ity (%)	length primary root (mm)	radicle emer- gence (%)	mortal- ity (%)	length primary root (mm)
<i>P. lanceolata</i> (2.4-1.0-0.8)*	31.9	83.3	$\bar{x}$ : 6.4 5.7-7.0	65.6	40.9	$\bar{x}$ : 12.0 8.6-15.5	84.4	0	0	93.7	51.4	$\bar{x}$ : 13.8 10.0-17.6
<i>P. media</i> (2.0-1.0-0.3)	58.2	64.9	$\bar{x}$ : 4.0 3.2-4.7	81.8	14.8	$\bar{x}$ : 3.3 2.4-4.1	75.3	0	0	74.3	19.1	$\bar{x}$ : 3.4 2.2- 4.5
<i>P. major</i> ssp. <i>major</i> (1.2-0.9-0.3)	88.7	58.8	$\bar{x}$ : 3.0 2.6-3.4	94.5	5.0	$\bar{x}$ : 1.8 1.3-2.4	97.4	0	0	98.2	1.5	$\bar{x}$ : 2.1 1.2- 3.0
<i>P. coronopus</i> (0.9-0.4-0.1)	77.5	7.3	$\bar{x}$ : 1.5 0.9-2.1	79.4	1.4	$\bar{x}$ : 0.9 0 - 1.9	70.6	0	0	80.9	0	$\bar{x}$ : 1.1 0.6- 1.5

\* mean length, width and thickness of the seeds (mm)

\*\* mean length ( $\bar{x}$ ) and 95% confidence interval

- All values are determined 14 days after sowing

- Radicle emergence: percentages of germinated seeds with reference to the numbers of sown seeds

- Percentages mortality with reference to numbers of germinated seeds

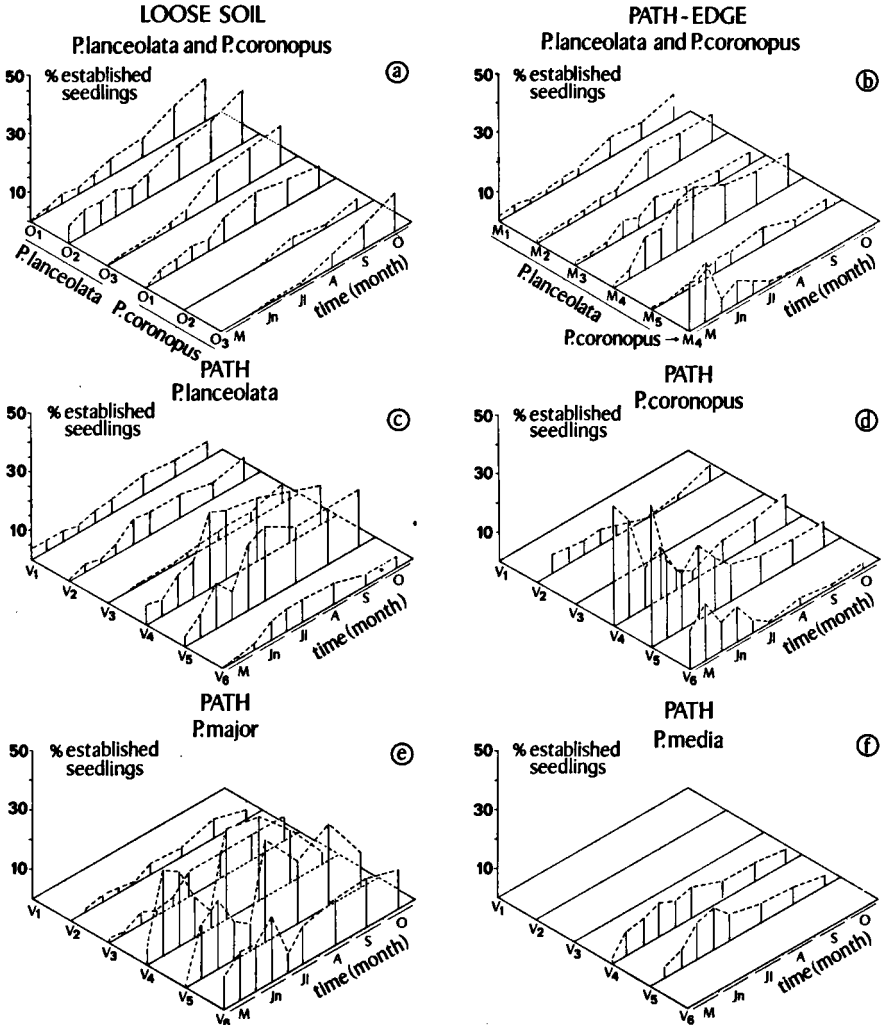


Fig. 1. Time course in percentages of established seedlings from seed sown in April 1974 on open plots with a loose soil (O<sub>1</sub>–O<sub>3</sub>), on path-edges (M<sub>1</sub>–M<sub>5</sub>; moderately compacted), and on paths (V<sub>1</sub>–V<sub>6</sub>; highly compacted) in a dune grassland. The percentages are given with reference to the numbers of seeds sown per species.

On the plots situated on the edges of paths (M<sub>1</sub>–M<sub>5</sub>) only *P. lanceolata* seedlings emerged reasonably well (fig. 1b). During the season three to four peaks in the mortality curves were observed (fig. 2b). Some *P. coronopus* seedlings were observed on plot M<sub>4</sub>, but in August none of the emerged plants survived (fig. 1b). Probably due to the high soil-moisture content of this plot some *P. major* and *P. media* seedlings were also found until August.



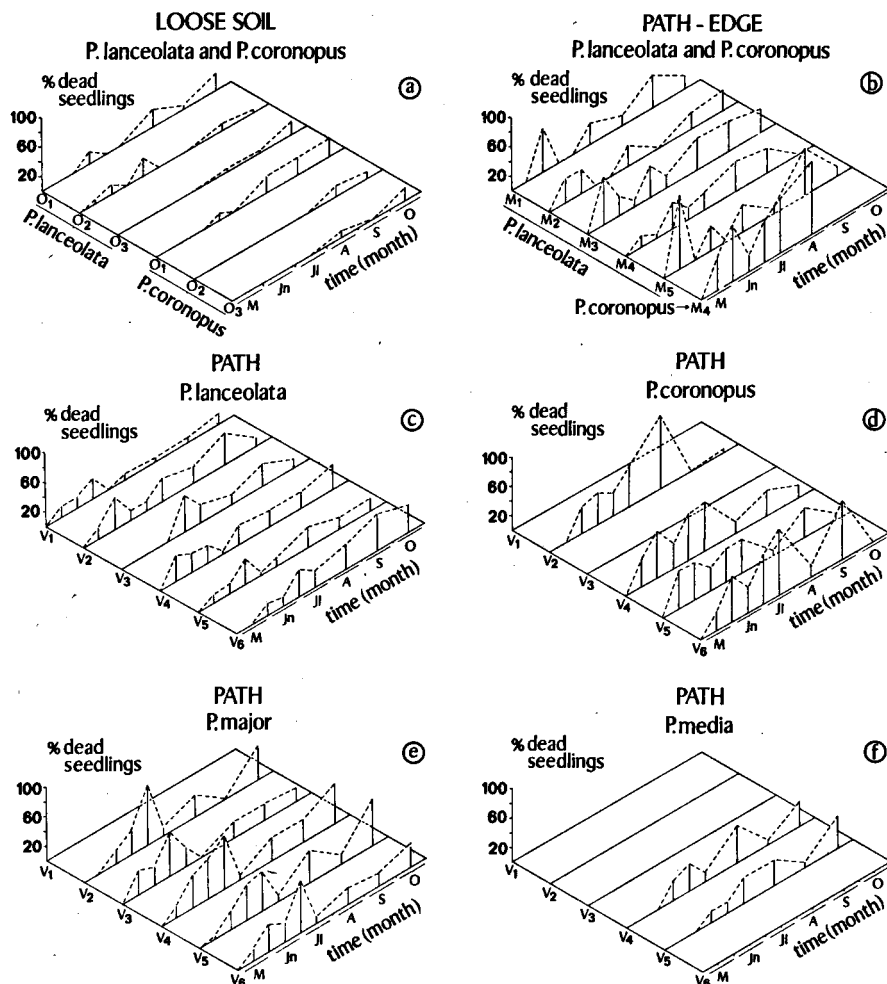


Fig. 2. Percentages of seedlings which died in eight periods during the growth season of 1974. On each date the percentages are calculated with reference to the numbers of emerged and established seedlings since the previous observation.

Due to a higher trampling intensity, the plots  $V_4$ ,  $V_5$ , and  $V_6$  were characterized by a vegetation layer which was lower and more open than on plots  $V_1$ ,  $V_2$ , and  $V_3$ . Furthermore, from these plots on the paths,  $V_1$  was relatively dry (mean soil-moisture content by weight 7.7%), whereas the soil of plot  $V_6$  appeared to be very wet (93.3%). For all species the highest numbers of seedlings were found on plots  $V_4$  and  $V_5$  (moderately wet and open). Only *P. major* occurred abundantly on the wet plot  $V_6$ , whereas on the dry plot  $V_1$  only *P. lanceolata* seedlings were present (figs. 1c, e). *P. coronopus* emerged in considerable numbers in the first two weeks after sowing on plots  $V_4$  and  $V_5$ , but a rapid fall in numbers of living seedlings was

Table 3. Numbers of living and percentages of dead (between brackets)\* *Plantago* plants in 1975 on plots in which the seeds were sown in April 1974.

<i>P. lanceolata</i>					
Plot	June	July	August	September	October
O <sub>1</sub>	12 (58.6)	16 ( 5.9)	14 (22.2)	12 (14.3)	9 (30.8)
O <sub>3</sub>	20 (39.4)	20 ( 4.8)	19 (13.6)	12 (33.3)	12 (14.3)
M <sub>1</sub>	18 (28.0)	17 (26.1)	14 (26.3)	17 (15.0)	18 (10.0)
V <sub>4</sub>	4 (86.7)	3 (25.0)	4 (20.0)	4 ( 0 )	3 (25.0)
V <sub>5</sub>	2 (95.1)	2 ( 0 )	1 (50.0)	0 (100)	0 ( - )
<i>P. coronopus</i>					
Plot	June	July	August	September	October
O <sub>1</sub>	12 (42.8)	13 (13.3)	16 ( 0 )	15 (11.8)	11 (31.3)
O <sub>3</sub>	13 (51.9)	11 (26.7)	17 ( 0 )	18 (18.2)	20 ( 9.1)
V <sub>4</sub>	1 (95.5)	1 ( 0 )	1 ( 0 )	1 ( 0 )	1 ( 0 )
V <sub>5</sub>	1 (96.3)	1 ( 0 )	1 ( 0 )	1 ( 0 )	1 ( 0 )
<i>P. major</i> ssp. <i>major</i>					
Plot	June	July	August	September	October
V <sub>4</sub>	8 (74.2)	13 (23.5)	9 (40.0)	11 ( 0 )	9 (25.0)
V <sub>5</sub>	6 (73.9)	12 (14.3)	7 (41.7)	7 ( 0 )	3 (57.1)
<i>P. media</i>					
Plot	June	July	August	September	October
V <sub>4</sub>	3 (76.9)	3 (40.0)	1 (66.7)	1 ( 0 )	0 (100)
V <sub>5</sub>	2 (80.0)	2 ( 0 )	2 ( 0 )	1 (50 )	1 ( 0 )

\* on each date the percentages of dead seedlings are calculated with reference to the numbers of emerged and established seedlings since the previous observation.

observed subsequently (fig. 1d). Two or three peaks can be recognized in the curves indicating established and dead seedlings of *P. major* and *P. coronopus*, but marked differences between both species were found (figs. 1d, e and 2d, e). In June, August and October a decrease in numbers of dead *P. coronopus* seedlings was found, whereas at that time a relatively high level of dead *P. major* plants was observed. It should be noted that more *P. major* seedlings were found after a spell of rainy days. During the season the emergence of *P. coronopus* in plots V<sub>2</sub> and V<sub>5</sub> occurred in significantly higher numbers than in the case of *P. major* ( $P < 0.05$ ). Especially from July onwards the numbers of living *P. major* plants were significantly higher than those of *P. coronopus* in all plots on the paths, which also indicates the high mortality of the *P. coronopus* seedlings.

The soil-moisture content of plots M<sub>4</sub> and V<sub>6</sub> appeared to be very high. In a preliminary experiment in the greenhouse, the radicle emergence and the growth of roots of *Plantago* seedlings were studied in pots with moderately-compacted and water-saturated, sandy soils. Important differences between species were

observed in percentages of germinated seeds. Twenty days after sowing the germination of *P. major* ssp. *major* had reached 41 per cent, followed by *P. coronopus* (20%), *P. lanceolata* (10%), and *P. media* (3.5%). Seedlings of all species were capable of penetrating the wet soil, but roots of *P. major* seedlings became much longer than those of the other species. After 45 days the mean length of *P. major* roots was 13 cm, whereas *P. lanceolata* and *P. media* roots reached a mean length of 4.5 cm. The roots of *P. coronopus* seedlings were still shorter (2.5 cm) but most lateral roots per unit-length were formed in this species. Lowest mortality was found in *P. major* and the highest in *P. coronopus*. The results of these preliminary experiments confirm the field observations, especially those of plot V<sub>6</sub> (figs. 1d, e and 2d, e).

Table 3 shows, for five plots, the numbers of plants which remained a year after sowing as well as the percentages of plants which had succumbed during five periods in 1975. In contrast with the other plots some individuals of *P. lanceolata* and *P. coronopus* in the O-plots had flowered in 1974; thus the emerged seedlings in those plots could have originated from seeds sown in 1974 or from seed produced in 1974. Marked differences were found for the four species; between October 1974 and June 1975 relatively high numbers of living *P. lanceolata* and *P. coronopus* plants on the O- and M-plots remained, whereas on the V-plots most individuals of these species had disappeared. On the V-plots many *P. major* and *P. media* plants had also succumbed between October 1974 and the first observation in 1975, but compared with the other species the percentages of dead plants were much lower. *P. media* disappeared nearly completely in the V-plots during 1975, whereas most *P. major* survived. The fall in numbers of *P. major* plants in October 1975 was also observed at the end of 1974 and can be explained by the fact that only upper parts of this species die off in autumn and winter. During 1975 emergence of *P. lanceolata* was observed in the O- and M-plots, *P. coronopus* emerged in the O-plots and *P. major* in the V-plots.

#### 4. DISCUSSION

The germination capacity of seeds is in general strongly dependent on the characteristics of the population from which the seeds are collected (cf. THOMPSON 1975). Differences in germination responses are even observed between seeds collected from different individuals (*Rumex crispus* cf. CAVERS 1974). SALISBURY (1965) reported on differences in germination of *P. major* seeds collected from different parts of the spike. Changes in size and shape of seeds can influence the processes of germination and establishment (HARPER et al. 1970). Due to different environmental conditions, shape, size and weight of seeds can differ markedly. This was shown by SALISBURY (1974) for 20 genera and which will be reported for *Plantago* species in a following paper by the present author. Thus the behaviour of seeds and seedlings as described in this paper must be considered as the characteristic reaction of seeds from populations occurring on the sites described under section 2.1. The percentages of *Plantago* seeds germinated under laboratory conditions (table 1) were in general higher than those mentioned in the literature, which can be

explained by the fact that either the seeds came from different populations or that tests of other authors were performed with relatively fresh seeds. KIGEL et al. (1977) reported on increasing ability to germinate in old seeds of *Amaranthus retroflexus*.

A feature of interest was the high susceptibility to weak green safelight of seeds of both *P. major* subspecies (*table 1*). Probably a very low level of the active form of phytochrome is sufficient to induce germination in these seeds. This level might be obtained by irradiation with green light (cf. SMITH 1973). This reveals that results of dark germination experiments in which seeds are exposed temporarily to weak green safelight can be different from results obtained in complete darkness, which was also recognized by J. P. Grime (personal communication).

The germination of the relatively large seeds of *P. lanceolata* increased at increasing size of particles which provided more suitable micro-sites and thus a better seed-substrate contact (*table 2*). Penetration of root tips depends on at least four physical characteristics of a substrate: bulk density, porosity, pore diameter and aggregate formation. With increasing particle size, the bulk density increases and the porosity decreases (STAPLE 1975). The diameter of pores increases markedly at increasing particle size (GOSS 1977). The primary roots of all species under study were more capable to penetrate substrates with the large particles; only the primary roots of *P. coronopus* penetrated rapidly the upper layer of the substrates with the small particles (*table 2*). The low capacity of the primary roots of *P. lanceolata* for penetration of the surface of the sandy soil can be explained by the fact that the degree of aggregate formation within this type of soil is higher than in case of substrates with round glass beads. As shown in *table 2*, the primary roots from small seeds (*P. coronopus* and *P. major* ssp. *major*) were more capable of penetrating the surface of the substrate than those of relatively large seeds (*P. lanceolata* and *P. media*). PIGGIN (1976) observed similar relations between seed size and soil-root penetration for seedlings of *Echium plantagineum* and *Trifolium subterraneum*. ASHER & OZANNE (1966) found, however, the reverse effect for several species.

As demonstrated earlier (BLOM 1976, 1977) the knowledge of the behaviour of plants in the various stages of their life-cycle is essential for a good understanding of their reaction to biotic and abiotic factors. Insight into the processes of seedling emergence and establishment during the course of time can be obtained by sowing experiments in the field (e.g. PEMADASA & LOVELL 1975 and this paper). The chance of survival strongly depends on the space available to the seedlings (ROSS & HARPER 1972). In the field experiments described in this paper, the distance between surviving seedlings appeared to be relatively large; only small numbers of seedlings emerged. This can be ascribed either to stress (moisture) or to disturbance (trampling). It is well known that these two factors cause a decrease in plant density (e.g. GRIME 1978). A low moisture content was limiting for the emergence of *P. major* and *P. media*, whereas *P. coronopus* seedlings did not survive intensive trampling (BLOM 1977). Most *P. lanceolata* plants occurring on plots situated on a path died the year after emergence (*table 3*). In the sowing experiments on the path, the strong decrease of living *P. coronopus* seedlings in the first week of June can be

ascribed to trampling; many walkers had been observed during this period. It is not known how many times the individuals of each species have been trodden but the supposition seems to be justified that a high trampling activity caused the death of many *P. coronopus* seedlings. To study the relation between trampling and survival more precisely, trampling experiments were performed in the greenhouse (BLOM 1977) and in the field by means of a trampling machine (BLOM, in preparation). The latter experiments showed that full-grown *P. coronopus* plants had a high resistance to trampling.

On compacted soils in the dunes, the humic sandy substrate is often wet (plots M<sub>4</sub> and V<sub>6</sub>). The question arises what will influence the establishment of seedlings more: the mechanical impedance of the soil, or the water saturation with a reduced oxygen content. In agricultural literature it has been demonstrated that the reaction of several species to these factors differs greatly (e.g. BARLEY et al. 1965; WARNAARS & EAVIS 1972; and HEMSATH & MAZURAK 1974). The preliminary experiments described in section 3 showed that the occurrence of the *Plantago* seedlings on very wet compacted soils depends on the germination capacity under these conditions as well as on the capability to penetrate the soil. *P. major* appears to meet these requirements best of all. It can be supposed that failure in germination may be ascribed to a low oxygen content due to the high water content, whereas the reduction of root growth is mostly caused by the mechanical impedance of the soil.

Only *P. lanceolata* seedlings established themselves reasonably well in the tall dense vegetation layer of the plots on the paths and on the path edges. *P. major* ssp. *major* was found in the least numbers under these conditions.

As will be reported in a following paper, the levels of nutrients in the soil of a path are mostly higher than those in the humus-poor loose sandy soils. The high level of established plants of *P. major* on the more open plots on the paths can be ascribed to this factor, since the growth of this species is strongly stimulated by a high nutrient level (KUIPER & KUIPER 1978). The results described in this paper as well as the findings of previous experiments (BLOM 1976, 1977) are summarized in table 4.

Table 4. The occurrence of seedlings of four *Plantago* species in relation to some environmental conditions in coastal sand dunes. 1 = lowest degree of the condition mentioned, 2, 3, and 4 = increasing degrees and occurrences; coron. = *P. coronopus*, lanc. = *P. lanceolata*, major = *P. major* ssp. *major*, media = *P. media*.

	LOW	1	2	3	4	HIGH
Degree of soil compaction		lanc.	media	coron.	major	
Trampling intensity		coron.	lanc.	media	major	
Soil-moisture level		lanc.	coron.	media	major	
Influence of surrounding vegetation		major	media	coron.	lanc.	

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