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4.2 Germination and Establishment

4.2.1 Germination of *Plantago* Species as Affected by Seed Age, Temperature and Light

Although the percentage of germination in *Plantago* seeds is high under laboratory conditions and in the field, there are environmental factors which strongly influence the germination capacity. Especially age of the seeds, temperature, illumination, and moisture content of the substrate are important for radicle emergence and seedling establishment.

Radicle emergence of fresh seeds was significantly lower than that of 1- to 5-year-old seeds (Table 4.7). The germination capacity of seeds older than 4 years strongly decreased. The results of Table 4.7 were obtained with seeds stored at room temperature. Sagar and Harper (1960) showed that a prechilling

Table 4.7. Germination percentages^a under different light conditions in relation to the age of dry-stored seeds of six *Plantago* species. All results were obtained at 25 °C 14 days after sowing. Most tests were performed with 10×50 seeds in each year

Seed age in years	0 ^b	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					

Table 4.7 (continued)

Seed age in years	0 ^b	1	2	3	4	5	6
<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

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

^b Freshly collected seeds.

a: Daily photoperiod 16 h light, 8 h darkness.

b: Complete darkness except for 2 min faint daylight daily.

c: Complete darkness except for 2 min faint green light daily.

d: Complete darkness.

–: Insufficient observations available.

treatment at 5 °C of fresh *P. major* seeds resulted in an increase of germination, whereas only small differences in germinability between prechilled and fresh seeds of *P. lanceolata* and *P. media* were found (Fig. 4.4); this was also observed for *P. coronopus* and *P. maritima*.

The influence of temperature on radicle emergence of plantains was also studied by Sagar and Harper (1960). The percentage germination of *P. media*

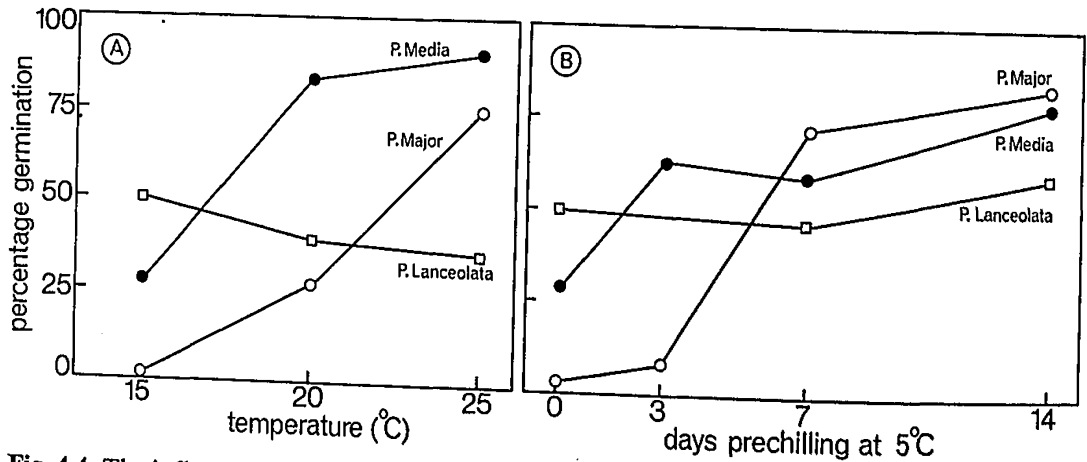


Fig. 4.4. The influence of temperature (A) and time of prechilling at 5 °C (B) on the germination of seeds of *Plantago media* (●), *P. major* (○) and *P. lanceolata* (□)

and *P. major* increased with a rise in temperature from 15 to 25 °C, especially between 15 and 20 °C (*P. media*) and 20 to 25 °C (*P. major*). Observations on *P. lanceolata* seeds showed no temperature effect; also seeds of *P. coronopus* and *P. maritima* were not affected. These results demonstrate that temperature was important for germination of *P. media* and even more so for *P. major*. The proportion of the seeds of *P. major* capable of germination strongly decreased when the temperature fell below 20 °C; the radicle emergence of fresh to 3-year-old seed did not exceed 3% and for older seeds 7% was obtained. Below 18 °C the radicle emergence of fresh *P. media* seeds was about 5%, and older seeds reached a mean germination of 12% (Sagar and Harper 1960, 1964; Blom 1978). A fluctuating temperature regime (15–20 °C) did not improve germination of seeds of all species, compared with a constant temperature of 25 °C (Blom 1978).

The data of Table 4.7 show that with the exception of *P. lanceolata*, *Plantago* seed germination was increased by 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 (25 °C), under so-called safe green light conditions considerable numbers of germinated seeds, especially seeds of *P. major* ssp. *major*, were observed. The influence of light on germination of *P. major* depends on the temperature (Harper and Sagar 1960). At 20 °C, only about 10% of the seeds germinated in light and no germination was found in darkness. At 25 °C, the percentage of germinated seeds in light was raised to about 25% and, contrary to our experiment, in the dark a few seeds germinated (5%). Hawthorn (1974) also found some germination of *P. major* in darkness. Since these results differ from the results found by Blom (1978, Table 1) germination characteristics of *P. major* may differ slightly between different populations.

4.2.2 Germination and the Effects of Moisture

The influence of moisture on germination of *Plantago* species was studied (Blom 1979; Fig. 4.5). At a low moisture content of the soil, dune sand, seeds of *P. lanceolata* and *P. coronopus* germinated. Maximum germination of *P. lanceolata* was found at 21% moisture level (by volume). Maximum germination of *P. coronopus* was observed between 11 and 21%. At a moisture level of 8%, 28% of the *P. maritima* seeds had germinated and a maximum of 91% was found at a moisture content of 21%. *P. major* ssp. *major* and ssp. *pleiosperma* were most sensitive to low moisture levels, followed by *P. media*. Maximum percentages of germinated seeds of these species were obtained at 21% moisture. In water-saturated dune sand all species germinated less and only a few germinated seeds were observed in *P. media* and in both subspecies of *P. major*. It is remarkable that at these circumstances relatively high numbers of seeds from the other species germinated.

4.2.3 Germination and the Effects of Soil and Other Substrates

Experiments on the germination capacity of *Plantago* species strongly suggested that differences in chemical soil conditions had no effects. For example, no important differences in maximum germination were observed when the seeds

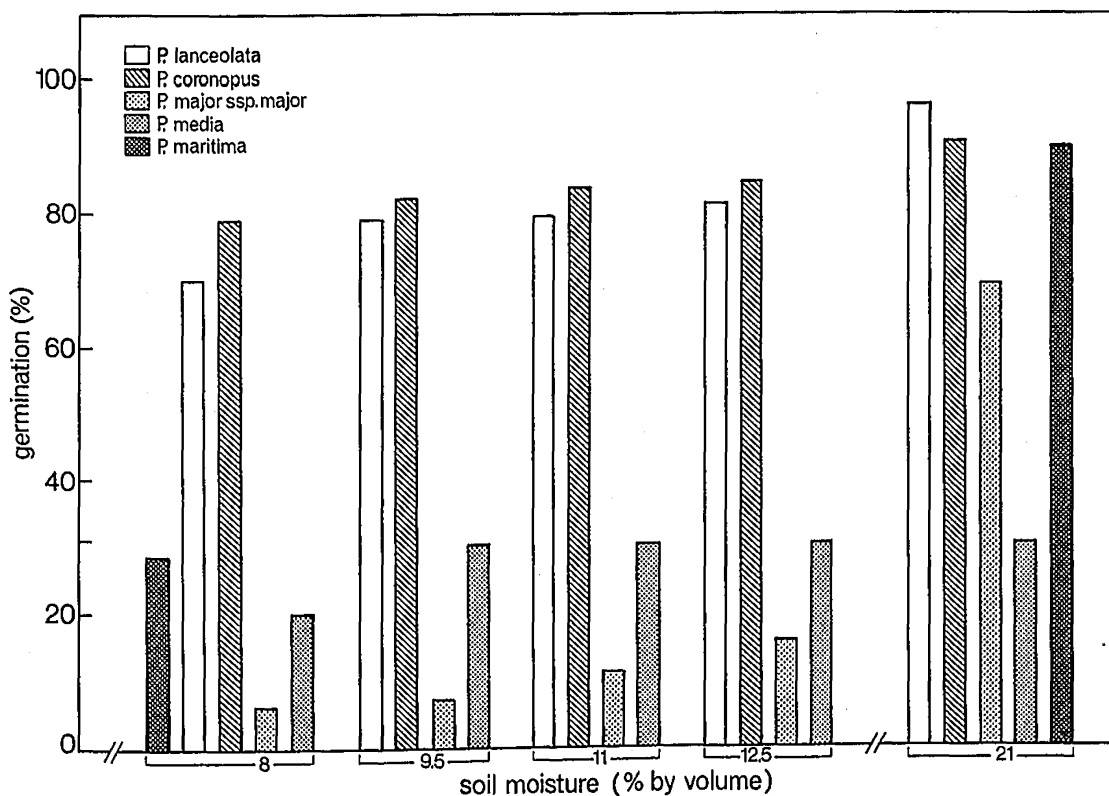


Fig. 4.5. The effects of different soil-moisture conditions on the germination of five *Plantago* species

were sown on pure sand, sand rich in organic matter, sandy clay or clay soils. Besides differences in germination capacity caused by other effects such as seed age, temperature, light conditions and soil-moisture content, physical soil characteristics appeared to be important. Sagar and Harper (1960) demonstrated dramatic differences in germination of *P. lanceolata* between a filter pad, 45% germination, vermiculite, 54% and soil, 72%. Similar results were obtained with seeds of *P. media* and *P. major*. Germination of seeds and seedling establishment in soils were strongly influenced by the size and shape of the seeds and by the microtopography and structure of the upper soil layers (McIntyre 1958; Parker and Taylor 1965; Taylor et al. 1966; Harper et al. 1970; Taylor 1962, 1971; Sheldon 1974; Oomes and Elberse 1976). For this reason a study using glass beads as a more simplified substrate for germination was performed.

Germination and establishment of the five *Plantago* species was studied by varying the size of the glass beads as substrate (Blom 1978). The second important factor in seed/substrate particle interaction was seed size. It decreased in the order *P. maritima*, *P. lanceolata*, *P. media*, *P. major* ssp. *major*, *P. major* ssp. *pleiosperma* and *P. coronopus*. Experiments were carried out in boxes filled with round glass beads of a diameter varying between 0.01 and 0.05 mm, 0.17 and 0.25 mm, and 0.89 and 1.23 mm. As a reference, boxes were filled with compacted dune sand, the particles varying between 0.05 and 1.0 mm with a median value of 0.19 mm (Table 4.8). Radicle emergence of *P. maritima*, *P. lanceolata* and *P. media* significantly increased with increasing size of the glass beads. No effect of glass bead size was found in the species with the smaller seeds. Mortality of the young seedlings was highest on substrate with the smallest bead size. On sandy soil and substrates with the low and intermediate bead size, mortality decreased with seed size. Death of seedlings was caused by the inability of the primary root to penetrate the dense substrate caused by the small beads; with exception of *P. maritima* and *P. lanceolata*, root penetration on the substrate with the small beads followed almost immediately upon radicle emergence. Penetration of the lower layers by the roots was relatively slow for *P. lanceolata*, *P. media* and *P. major* ssp. *major* resulting in a high mortality. The primary roots of *P. maritima* and *P. lanceolata* (both with large size of seeds) penetrated the dense substrate with small beads and the sandy soil more effectively. The roots "meandered" over the bead surface to find a gap for penetration (see also Sheldon 1974). On the sandy soil, many laterals penetrated the surface; however, a high mortality was not prevented (*P. maritima*, unpubl. results).

Compaction appeared to be a most important factor influencing germination of *Plantago* (Blom 1979). Laboratory experiments at an optimal soil-moisture level showed the highest percentages of emerged *Plantago* seedlings on loose soils; at low moisture levels the highest numbers of seedlings were observed on the compacted soils. These results were clearly evident in both subspecies of *P. major*.

In another experiment seeds were sown in turves collected in the field and brought to the laboratory (Blom 1977). Germination of all species increased

Table 4.8. Effect of substrates of different particle size on the seedling radicle emergence, seedling 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 emergence (%)	Mortality (%)	Length ^b primary root (mm)	Radicle emergence (%)	Mortality (%)	Length primary root (mm)	Radicle emergence (%)	Mortality (%)	Length primary root (mm)	Radicle emergence (%)	Mortality (%)	Length primary root (mm)
<i>P. lanceolata</i> (2.4–1.0–0.8) ^a	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) ^a	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) ^a	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) ^a	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

^a Mean length, width and thickness of the seeds (mm).

^b 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.

– Percentage mortality with reference to numbers of germinated seeds.

with increasing compaction of the soil, especially in species with large seeds and with *P. major*. This may be probably ascribed to an increased water availability of compacted soils. The increase in water-holding capacity by soil compaction was also observed by Liddle and Greig-Smith (1975) for dune sand and by Krüger (1970) for diluvial loamy sand and alluvial meadow soil. Since seedlings emerged on the turves under competition, a high mortality should be attributed to competition from the neighbouring plants.

In this experiment high percentages of dead *P. major* and *P. media* seedlings were observed and the other *Plantago* species were less affected. Also, in the experiment with the turves, a trampling treatment was applied (Blom 1977). Due to a light trampling treatment an increase in germination occurred in *P. lanceolata* and *P. media*. Apparently, the large seeds were pressed into the soil by the light trampling, which resulted in a better seed-soil contact and more seeds being germinated. Such effects were absent in species with smaller seeds.

4.2.4 Emergence and Establishment Under Field Conditions: *P. lanceolata*, *P. coronopus*, *P. major*, *P. media*

Laboratory tests are necessary to understand germination, emergence and seedling establishment in the field. To bridge the gap between laboratory conditions and the field, experiments in artificial plots in the field are useful (Blom 1976). Germination experiments were performed in open plots in an experimental garden. The original soil was removed and replaced with dune sand, poor in organic matter, which was compacted to various degrees. Soil moisture depended on rainfall.

Seedlings of *P. lanceolata* and *P. coronopus* emerged in highest numbers on the least compacted soils; seedlings of *P. major* and *P. media* were found in the highest numbers on the more compacted soils and after two years no *P. major* plants survived the loose soil habitat (Fig. 4.6). The opposite reactions 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 mechanical resistance and moisture. The soil moisture of these barren sand plots in general was very low. Since *P. lanceolata* and *P. coronopus* germinate better at low soil moisture than *P. major* and *P. media*, soil moisture probably is more limiting for germination for the latter two species. This conclusion also explains the fact that the emergence of *P. major* and *P. media* seedlings was higher on the compacted soils. Mechanical resistance was an important limiting factor for the emergence of *P. lanceolata* and *P. coronopus* seedlings. The low number of seedlings on the intermediate compacted soils was possibly due to relatively large resistance in combination with a relatively low water availability.

Factors interrelated with soil compaction are mechanical resistance, availability of moisture, aeration and 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.

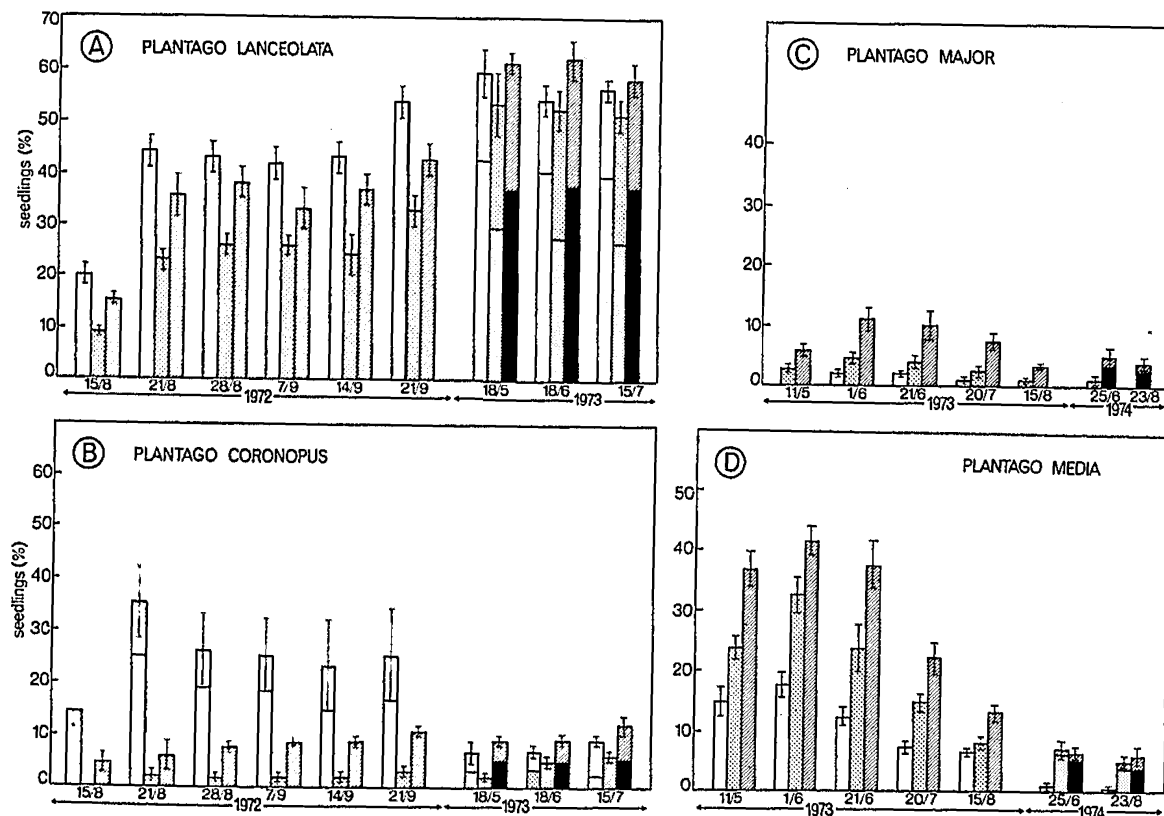


Fig. 4.6. The influence of soil compaction on seedling emergence from buried *Plantago* seeds in experimental plots in the field (mean values of four comparable plots). For the columns on the right a distinction was made between newly emerged plants and plants of the preceding year, the upper part representing the former and the lower part the latter. The vertical bars represent twice the standard deviation. □ Loose soil; ▨ moderately compacted soil; ■ compacted soil

Structure of the upper soil layers, mechanical resistance and soil moisture are considered as most important for germination.

To analyze the effect of the environment on establishment of *Plantago*, Sagar (1959) and Sagar and Harper (1960) carried out a series of experiments in which seeds of *P. major*, *P. media* and *P. lanceolata* were sown in a range of habitats which represented plant communities from which plantains were absent and communities in which they normally occurred. In acid heath and valley bogs only few seeds germinated and emerged seedlings succumbed. In beech and oak woodland communities germination was low and seedlings died quickly, probably due to lack of light. In open arable land, without naturally occurring plantains, all species germinated in relatively high numbers, but only *P. lanceolata* seedlings survived. In open grassland on exposed limestone, without naturally occurring plantains, all species germinated and after 1 year all seedlings had succumbed to drought. No germination was found in tall grass habitats, which was ascribed to the absence of light for *P. media* and *P. major*. The fact that *P. lanceolata* was unable to establish itself in its own habitat remains unexplained. Possibly seeds from a meadow ecotype were used. In a similar experiment emergence and establishment were studied by sowing seeds in a dune area (Blom 1977) on paths with compacted soils and partly covered by

vegetation (V-plots, Table 4.9), on the edges of paths with moderately compacted soils (M-plots) and a tall, dense vegetation, and on loose soils with an open vegetation (O-plots). In general, an increase in emergence was found at increasing trampling intensity and soil compaction (Table 4.9).

Seedlings of *P. coronopus* did not survive intensive trampling, whereas full-grown plants had a high resistance to trampling. More plants of *P. lanceolata* survived on paths than would be expected (Blom 1979); fluctuations in trampling probably increased survival. In open arable land only *P. lanceolata* seedlings survived (Sagar and Harper 1960). *P. lanceolata* seedlings also emerged reasonably well in the tall dense vegetation of the M-plot. Seedlings of *P. coronopus* are often observed in gaps between stones where they are protected against trampling. The highest numbers of surviving *P. major* seedlings were found on open, trampled sites. On the plots with a relatively dry soil, *P. major* and *P. media* remained absent. The occurrence of seedlings on wet compacted soils will depend on the germination capacity and the capacity to penetrate the soil. *P. major* clearly met these requirements and the failure in germination by the other species may be ascribed to a low oxygen content, and inhibited root growth by mechanical impedance of the soil.

4.2.5 Emergence and Establishment Under Field Conditions: *P. maritima*

Survival of seedlings of *P. maritima* was studied by Jerling (1981) on a Baltic seashore meadow; it was related to a topographical gradient from 15 to 54 m from the seashore and to topographical changes in the microhabitat.

Seedling mortality in pre-summer was probably due to desiccation. The seedlings near to the sea suffered more from drought than those found more inland. This may be due to a reduction in vegetation density at the seaside. Later in the year, flooding caused death of the seedlings, especially in the seaside zone. Mortality occurred especially after flooding, but differences in the length of the inundation period due to the differences in microtopography could not explain the observed differences in mortality. Jerling (1981) suggested that light deficiency due to the deposition of iron and salts (FeS , Fe^{3+}) and toxic effects of H_2S caused mortality.

Further studies on *P. maritima* seedlings along the gradient in a seashore meadow by Jerling (1982, 1985 a) showed that survival of seedlings was closely related to vegetational characteristics such as total cover, height of vegetation and amount of litter, all factors resulting in reduced light. Superimposed on these characteristics was the duration of flooding. Furthermore, the mortality was positively related to a high density of populations of *P. maritima* seedlings and juvenile plants. It can be concluded that establishment and survival were closely dependent on the availability of "safe" sites as spots lacking high vegetation and spots with a large amount of litter. The number of "safe" sites depended on factors as grazing pattern, deposition of litter by the sea, etc. The number of open and "safe" spots increased approaching the seaside together

Table 4.9. Some environmental factors relating to the emergence and mortality of *Plantago* seedlings from seed sown in plots in the dune area on Voorne (The Netherlands)

Plot	Mean height vegetation (cm)	Cover (%)	Mean penetrometer values \pm S.E. at a depth of 5 cm (kg/cm ²)	Trampling intensity ^a	Soil moisture 0–5 cm (% dry weight)			Emerged seedlings and dead plants ^b			
					Lowest values	Highest values	Mean values	<i>Plantago lanceolata</i>	<i>Plantago coronopus</i>	<i>Plantago major</i>	<i>Plantago media</i>
O ₁	0	0	0.9 \pm 0.4	–	1.1	6.5	4.4	21.5 (32.5)	16.5 (54.5)	5 (100)	2 (100)
O ₂	5	50	5.6 \pm 2.1	–	2.0	7.5	4.2	24.5 (24.5)	7 (35.7)	0	0
O ₃	0	0	1.7 \pm 0.9	–	3.0	16.1	9.9	17.5 (22.9)	16 (18.7)	2 (25)	0.5 (0)
M ₁	15	100	10.8 \pm 2.3	\pm	4.4	39.4	13.7	17.5 (51.4)	0	1 (100)	3 (50)
M ₂	15	90	14.4 \pm 2.4	\pm	11.6	46.4	27.1	17 (47.1)	6.5 (84.6)	1 (100)	0
M ₃	10	100	6.6 \pm 1.3	\pm	42.8	104.2 ^c	70.8	19.5 (76.9)	16 (100)	2 (100)	0.5 (100)
M ₄	10	100	4.5 \pm 1.5	\pm	50.8	136.8 ^c	93.5	42 (72.6)	45 (100)	11.5 (100)	6.5 (100)
M ₅	10	100	5.2 \pm 1.7	\pm	34.6	95.5	60.1	12 (70.8)	2.5 (100)	8.5 (94.1)	2.5 (100)
V ₁	7	85	17.1 \pm 2.0	+	0.1	15.2	7.7	10.5 (42.8)	5.5 (100)	1 (100)	1.5 (66.6)
V ₂	5	70	26.8 \pm 6.2	++	20.5	60.4	43.4	22.5 (64.4)	25.5 (76.4)	11.5 (69.6)	2 (100)
V ₃	5	70	31.1 \pm 8.8	++	11.9	75.0	39.2	10.5 (38.1)	4.5 (100)	21.5 (60.5)	1 (100)
V ₄	2	40	21.0 \pm 5.8	+++	20.5	76.4	38.7	52 (74)	89 (87.6)	99.5 (95.5)	24.5 (79.6)
V ₅	3	50	22.5 \pm 3.6	+++	23.2	41.4	31.4	50 (61)	95 (90.5)	85.5 (86.6)	20 (80)
V ₆	3	40	17.8 \pm 1.9	+++	45.3	104.3 ^c	93.3	24 (83.3)	51 (97.1)	71 (80.3)	5.5 (90.9)

^a Symbols: trampling: – absent; \pm sometimes; + moderate; ++ rather frequent; +++ very frequent.

^b Emerged seedlings expressed as percentages of sown seed. In brackets: dead plants (%) calculated with reference to the total numbers of seedlings which had emerged during the test (April–October 1974).

^c Water table +1 cm above soil level at the end of October 1974.

Table 4.10. The optimal occurrence of seedlings of five *Plantago* species in relation to some environmental factors

Environmental factor	Low	Ranking			High
	1	2	3	4	5
Temperature	<i>lanc.</i>	<i>coron.</i>	<i>mar.</i>	<i>media</i>	<i>major</i>
Light	<i>coron.</i>	<i>major</i>	<i>media</i>	<i>lanc.</i>	<i>mar.</i>
Soil moisture	<i>coron.</i>	<i>lanc.</i>	<i>mar.</i>	<i>media</i>	<i>major</i>
Soil compaction	<i>lanc.</i>	<i>mar.</i>	<i>media</i>	<i>coron.</i>	<i>major</i>
Trampling	<i>coron.</i>	<i>lanc.</i>	<i>mar.</i>	<i>media</i>	<i>major</i>
Competition	<i>major</i>	<i>media</i>	<i>mar.</i>	<i>coron.</i>	<i>lanc.</i>
Flooding	<i>media</i>	<i>lanc.</i>	<i>major</i>	<i>coron.</i>	<i>mar.</i>

1 = lowest degree of the condition mentioned, 2,3,4,5 = increasing degrees.

coron. = *P. coronopus*; *lanc* = *P. lanceolata*; *major* = *P. major* ssp. *major*; *media* = *P. media*; *mar.* = *P. maritima*.

with the occurrence of flooding (frequency and duration). During years with long-lasting high water, floods will recede the seaside border of plantain establishment from the sea; simultaneously open and "safe" sites with sufficient light will be produced (Ericson 1980).

In a sowing experiment with *P. maritima* in a salt marsh (Blom 1983), it was observed that the seedlings emerged relatively quickly, and that the number of surviving seedlings was low. Heavy trampling and, to a lesser extent, daily flooding were important for seedling mortality. A relatively low mortality was observed in dense vegetation moderately trampled by cattle. The highest survival of seedlings was found on open and sandy soils. Seedling emergence increased markedly after rainfall, which undoubtedly was due to a decrease in soil salinity. In a germination experiment in the greenhouse it was observed that seedling emergence decreased strongly at a salinity higher than 25‰ of the salt concentration of seawater. Clearly, regularly flooding and heavy trampling caused mortality of *P. maritima* seedlings. The susceptibility of these seedlings to trampling is intermediate between *P. media* and *P. lanceolata*.

The occurrence of the *Plantago* species in relation to the important environmental factors were discussed in this section and summarized in Table 4.10.

4.3 Photosynthesis of *Plantago lanceolata* Populations in the Field

This section compares growth characteristics and photosynthetic response to light intensity of plants of *Plantago lanceolata*. Two contrasting habitats were chosen: the dry dune grassland, Westduinen, and the wet hayfield, Merrevliet. The habitats represent extremes in the distribution of *P. lanceolata* (Sect. 3.1).

The dune grassland microclimate can be classified as dry and warm (Sect. 3.3): during the day it is strongly influenced by convection as a result of heating of the soil by radiation. The hayfield microclimate was humid and