Establishment of *Plantago lanceolata* L. and *Plantago major* L. among grass *

II. Shade tolerance of seedlings and selection on time of germination

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Summary. Establishment of *Plantago lanceolata* and *P. major* ssp *major* among grass was studied in a field experiment in which survival and selection on date of seedling emergence and plant size was investigated in relation to the vegetation structure. *P. major* – in contrast to *P. lanceolata* – was not able to establish itself in grass because of its lower competitive ability caused by later germination, smaller seedling size, and shorter leaves. In both species there was selection for early germination. For *P. lanceolata* a significant correlation was found between the strength of selection and the light climate, determined by the structure of the grass sward. Plants that germinated early were at an advantage because they were larger, especially the leaves, when compared with plants that germinated late. It seems likely that selection was mainly by competition for light. Contrary to expectation *P. major*-seedlings had a higher shade tolerance than those of *P. lanceolata*. The performance of both species is discussed in relation to their different life strategies.

Key words: Germination – *Plantago* – Selection – Shade tolerance – Vegetation structure

The seedling stage of the life cycle is often characterized by high mortality. However, there is little data available about natural selection occurring in or shortly after this stage (Endler 1986). To study natural selection, it is essential to distinguish between selection and response to selection (Arnold and Wade 1984). Selection causes changes within a generation in phenotypic distribution of plant characteristics. However, evolutionary response to selection also depends on the inheritance of the relevant characteristics.

Selection in the field has been shown to act on the timing of germination. Early germinating plants often are relatively large and have high fecundity, in some cases combined with high (Cook 1980; Kalisz 1986; Miller 1987), but in other cases with low survival rates (Baskin and Baskin 1972; Marks and Prince 1981; Van der Toorn 1982). The results of a field experiment are reported here, in which selection for date of seedling emergence was studied during the juvenile stage. Two related species were used, viz. *Plan-*

tago lanceolata L., a species of closed turf, and *Plantago major* L. ssp *major* (further referred to as *P. major*), a colonist of bare soil. Both species are perennial herbs with leaves arranged in a rosette. *P. lanceolata* has larger seeds than *P. major* (mean weight of seeds used in this study: 1.53 and 0.31 mg respectively). In the first paper of this series concerning the germination behaviour of both species (Pons and Van der Toorn 1988), some results of the field experiment have already been discussed. In this paper, further results of the same experiment are reported. When sown in a grass sward *P. lanceolata* establishes reasonably well, in contrast to *P. major* (Blom 1978, 1979; Sagar and Harper 1961, 1964). The former species is expected to exhibit a different growth strategy when compared with the latter, viz. a higher competitive ability (Fenner 1978a) and a greater capacity to escape shade by elongation of cotyledons and leaves (shade avoidance strategy *sensu* Grime and Jeffrey 1965). Furthermore, *P. lanceolata* seedlings are expected to be more shade tolerant than those of *P. major* (Fenner 1978b). The response of seedlings to a low photon flux density was measured to test the latter hypothesis.

Materials and methods

Field experiment

The experiment which was performed from October 1981 till May 1983, was laid out in a hayfield on heavy clay soil. The sward was dominated by the following species: *Poa trivialis* L., *Phleum pratense* L., *Alopecurus pratensis* L., *Trifolium repens* L. and *Ranunculus repens* L. Both *Plantago* species occurred at low densities but were absent in the experimental plots. At the start of the experiment the structure of the sward was manipulated (within one square meter plots) by clipping the grass and making gaps in it. The grass was clipped weekly at 5 cm (treatment H5) and 15 cm (H15). *Plantago* plants were not clipped. The natural vegetation (HN) was maintained in unclipped control plots. Gaps were created by removing the above-ground vegetation both from central subplots measuring 5 × 5 cm (G5) and 10 × 10 cm (G10), respectively, and from whole plots (GL). Other species were removed from these gaps during the first winter and spring. All plots were arranged in a randomized block design with 5 replicates. As part of the routine management of the field as a whole, all plots were mown at about 5 cm high in mid June and the end of September.

Table 1. Survival and flowering of *P. lanceolata* (L) and *P. major* (M) in treatments with different vegetation structure. When survival rates for the periods 26/5–20/7/1982 and 20/7–20/9/1982 are compared (using a log-linear model), significant differences appear between species ($P<0.001$), treatments ($P<0.001$), and periods ($P<0.05$). Species × period and species × treatment interaction are significant at $P<0.001$ and <0.05, respectively

Treatment		Percentage survival						Percentage flowering plants (1/5/1983)	
		1982				1982/83			
		26/5–20/7		20/7–20/9		20/9–1/5			
		L	M	L	M	L	M	L	M
Vegetation	whole plot (GL)	85	88	–	–	–	–	91[a]	68[a]
removed	10 × 10 cm (G10)	90	83	95	72	56	0	37	–
from	5 × 5 cm (G5)	92	77	90	45	46	0	38	–
Vegetation	5 cm (H5)	66	60	91	69	63	0	50	–
kept at a	15 cm (H15)	65	35	76	17	21	0	33	–
height of	natural (HN)	42	53	65	45	60	0	17	–

[a] Measured on 20/7/1982
– = Not measured

Growth of the grass vegetation was very slow in March and April, but accelerated from early May onwards. The height of the sward (about 5 cm in early May) increased to about 15 cm on 20/7 and 25 cm on 20/9/1982.

Seeds of both species were collected randomly in a neighbouring grassfield during the first half of October 1981 and sown on 24/10/1981. In each plot 50 seeds per species were sown; each species in separate areas of 0.01 m².

Seedling emergence was observed at weekly intervals from early February till the end of May 1982. Seedling cohorts of each week were marked using coloured pins and monitored periodically up to May 1983. So many pins got lost during the winter period, that the influence of germination date on survival and selection processes could only be analyzed for the first year (till 20/9/1982).

In contrast to all other treatments the growth of both *Plantago* species in the bare treatment (GL) was very vigorous, leading to fully developed plants in July 1982 (Table 1). As the plants had formed many side rosettes and density was high, development of individual genets could not be followed further and monitoring of this treatment was discontinued on 20/7/1982.

Measurements on plant morphology (length of cotyledons, length and width of longest leaf and number of leaves) were made at 2-weekly intervals (period 6/4–26/5/1982) and at 2-monthly intervals (20/7–20/9/1982) using subsamples of 2 and 3 replicate plots, respectively. As the measurements of 20/7/1982 consisted of the most individuals, they were used to analyze selection on various plant characteristics (Tables 3, 4).

Transmission of red light was measured on 26/5, 20/7, and 20/9/1982 with the red/far-red ratio sensor as described in Pons and Van der Toorn 1988.

Data analysis

Selection on phenotypic characteristics within generations can be quantified in several measures, describing different aspects of the relation between characteristic and fitness. Here we restrict ourselves to the selection differential and the selection intensity (Falconer 1981). The selection differential (S) measures the change in the mean value of a char-

acteristic, due to selection in the stage to which the fitness measure applies, according to the formula:

$$S = cov(z,W)/\bar{w}$$

in which z is the relevant characteristic, W a measure of fitness, and $\bar{w}$ the mean value of the fitness measure. During the vegetative stage survival is taken as a measure of fitness, which could be either 0 (dead) or 1 (alive). Significance of the selection differential is inferred from the significance of the regression of relative fitness (W/$\bar{w}$) on the relevant character (the so-called directional selection gradient; Lande and Arnold 1983). The selection intensity (i) is a standardized form of the selection differential. It is measured as:

$$i = S/\sigma_z$$

and is used to compare selection differentials. We do not suggest that selection between generations can be predicted from these measures of selection. They merely serve to detect which traits are important for fitness at a certain life stage.

Statistical analysis of survival data of the field experiment was carried out by means of a log linear model (Bishop et al. 1975). Plant measurement data of the same experiment were analyzed by the usual ANOVA. Analysis of RGR data of the low photon flux density experiment (see below) was carried out by ANOVA as described by Poorter and Lewis (1986).

Experiment on the influence of low photon flux density

The experiment was carried out in a plant growth chamber with a temperature regime of 12°/22° C and a 14 h thermo- and photoperiod. Light (Philips HPI 400 Watt) was filtered through a neutral density screen varying in density, which provided a range of low photosynthetic photon flux densities (PPFD): 0; 0.9; 2.5; 5.1 and 13.1 μmol m^{-2} s^{-1}. Seeds of both species (same collections as used in the field experiment) were allowed to germinate under the experimental conditions of 5.1 μmol m^{-2} s^{-1}. After four days recently germinated seeds were planted in pots with sand soaked in a nutrient solution and allowed to leak out. There were
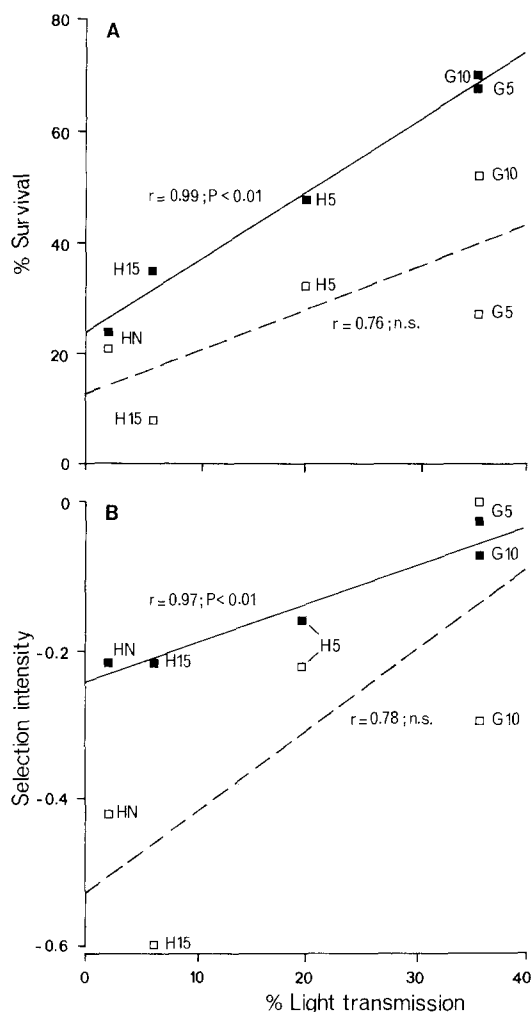
Fig. 1A, B. Survival (A) and selection intensity on date of seedling emergence (B) during the period 3/3–20/9/1982 for *P. lanceolata* (■——) and *P. major* (□– – –) as a function of the transmission of red light (measured on 26/5/1982). For legend of treatments see Table 1
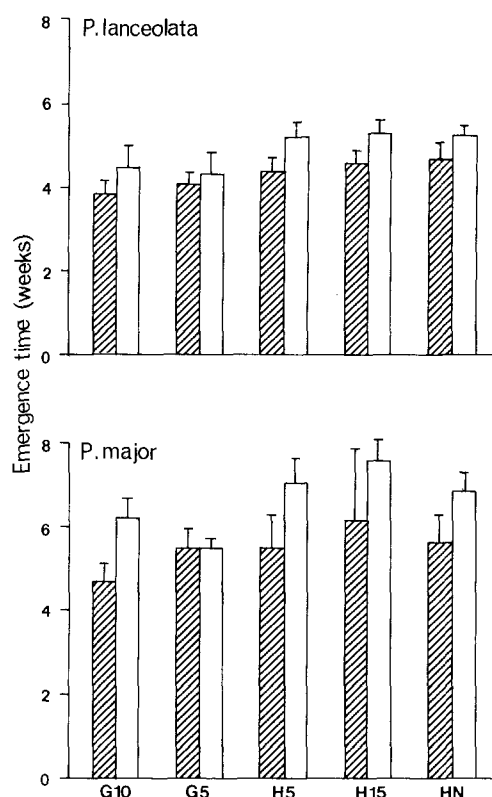

Fig. 2. Mean and standard error of date of seedling emergence (in weeks from 3/3/1982 onwards) for *P. lanceolata* and *P. major* in treatments with different vegetation structure (legend see Table 1). Plants are divided according their survival in the 3/3–20/9/1982 period (hatched = surviving; blanc = dead plants). Significant differences (ANOVA) exist between species ($P < 0.001$), treatments ($P < 0.001$), and surviving versus dead plants ($P < 0.01$)

4 plants per pot (7 × 7 cm) in the case of *P. lanceolata* and 9 in the case of *P. major*. Dry weights were determined of seeds and of seedlings at 21 and 49 days after germination in 8 replicates. The plants of one pot were weighed together excluding the seed coats. Relative growth rates (RGR) were calculated only when mortality did not exceed 10 per cent.

Results

Field experiment

Survival and establishment. As was reported in the first paper of this series (Pons and Van der Toorn 1988), seeds of *P. lanceolata* germinated over a 12-week period (3/3 to 26/5) and those of *P. major* over a 10-week period (18/3 to 26/5), respectively, showing that the former species germinated earlier (c.f. Fig. 2). Further, *P. lanceolata* showed a higher germination rate than *P. major* especially in closed vegetation.

Both species also showed significant differences in the survival rate of seedlings (Table 1). They reacted differently during the late summer period (species × period interac-

tion), resulting in higher survival rate of *P. lanceolata* when compared with *P. major*. This continued during the winter resulting in a disappearance (the following spring) of *P. major* from all treatments except GL (in this treatment fully grown and flowering plants were already present a few months after germination; c.f. Table 1). In contrast, *P. lanceolata* established itself by forming flowering plants in all treatments. Both species also showed significant treatment effects, which were related to availability of light. This can be characterized by the transmission of red light, giving high values for open and low values for closed vegetations. The survival of *P. lanceolata* in the first year appears to be correlated significantly with the light transmission, the mortality increasing under more shaded conditions (Fig. 1A). A similar, but not significant trend exists for *P. major*. No correlation was found between these survival data and light measurements during July and August, presumably because (in the case of *P. lanceolata*) most losses had occurred during early summer.

Selection on date of seedling emergence and plant size. Plants that germinate early have a higher survival rate (Fig. 2) and with both species a significant selection for early germination is found (Table 2). Selection is relatively more intense for *P. major*. Furthermore, for both species selection is more severe in closed than in open vegetation. As indicated by the selection differentials, the change in mean ger-

mination date due to selection (in closed vegetation), amounts to 0.4 week for *P. lanceolata* and 1.1 week for *P. major*. In addition, a significant correlation is found between the selection intensity and light transmission for *P. lanceolata*, whereas a similar, but not significant trend is found for *P. major* (Fig. 1 B). No correlation was found with light measurements of July and August, presumably for the same reason as in the case of the survival data.

To find out how selection on germination date actually worked, the selection for various characteristics was quantified separately for plants measured on 20/7/1982 (Table 3). The results indicate that especially selection for biomass and related traits (number and length of leaves) is important. Plastochron rate, a measure for growth in the number of leaves, seems to be less important, as is also the case for cotyledon length. The low selection intensity indicates that seed size, which is closely related to cotyledon length (Van Groenendael 1985), did not play a significant role in determining seedling success. Therefore, it can be concluded that selection on date of emergence is mainly determined by selection on plant size. As mentioned above, leaf length is one of the selected characteristics. Leaves of both species are relatively short (Table 4) in comparison to the height of the sward (being about 15 cm on 20/7/1982). It is understandable that under such conditions individuals

are favoured which have longer leaves as they intercept more light.

Plants in closed vegetation differed from those in gaps by a greater length of cotyledons and leaves and by a larger length:width ratio (Table 4). It seems likely that this is mainly caused by a plastic response to the different light climate. For leaf length and length:width ratio the response is relatively more pronounced for *P. lanceolata* (ratio closed vegetation:gap for the relevant traits in case of the surviving plants being respectively 1.1 and 1.5 for *P. lanceolata* and 0.9 and 1.2 for *P. major*).

Experiment on the influence of low PPFD.

Seedlings of *P. lanceolata* had a lower RGR during the first 21 days at the various PPFD used than seedlings of *P. major*. The difference largely disappeared during the second period of 28 days, because the RGR of *P. lanceolata* increased more than that of *P. major* (Fig. 3 A). At a PPFD where a negative RGR was measured during the first period, the mortality of the seedlings appeared to be very high during the second period. This resulted in a much higher mortality of *P. lanceolata* at 2.5 μmol m^{-2} s^{-1} compared to *P. major* (Fig. 3 B).

Discussion

A positive correlation between seed weight and survival of seedlings in darkness or shade has been reported by several authors (Grime and Jeffrey 1965; Hutchinson 1967; Verkaar and Schenkeveld 1984). Furthermore, seedlings of species from closed turf (Fenner 1978b) and woodlands (Hutchinson 1967) were found to be more tolerant towards darkness or shade than ruderals. In the low photon flux density experiment, however, the seedlings of *P. major*, the species from more open habitats with small seeds, were more shade tolerant than the seedlings of *P. lanceolata*, the species from closed turfs with larger seeds. The higher shade tolerance of *P. major* could be related to the fact that its broad horizontal cotyledons and leaves intercept light more effectively under the experimental conditions than the slender vertical cotyledons and leaves of *P. lanceolata* (c.f. Table 4). The seedlings of the latter species could not maintain their erect position at the lower PPFD, but in a dense vegetation the surrounding plants provide sup-

Table 2. Selection on date of seedling emergence for *P. lanceolata* and *P. major* (period 3/3–20/9/1982) in gaps (treatments G10 and G5) and closed vegetation (treatments H15 and HN)

Selection measure	P. lanceolata		P. major	
	Gap	Vege-tation	Gap	Vege-tation
N	219	213	162	67
Selection differential (weeks)	−0.133	−0.413	−0.394	−1.066
Selection intensity	−0.054	−0.219	−0.201	−0.523
P		**	**	*

Significance (*P*) indicated respectively as: *,** = *P* < 0.10, < 0.05
N = Number of seedlings

Table 3. Selection intensity of various traits for *P. lanceolata* and *P. major* (period 20/7–20/9/1982) in gaps (treatments G10 and G5) and closed vegetation (treatments H15 and HN)

Character	P. lanceolata		P. major	
	Gap	Vegetation	Gap	Vegetation
N	98	49	58	33
Seedling emergence date	−0.060*	−0.190	−0.162	−0.330
Cotyledon length	0.001	0.122	0.293	0.032
Leaf length	0.132***	0.253**	0.580***	0.330
Leaf length:width ratio	0.069	−0.070	0.081	0.201
Number of leaves	0.093**	0.106	0.429**	0.259
Biomass index	0.105***	0.211*	0.580***	0.431
Plastochron rate	0.108	0.014	0.301	−0.014

Significance indicated as: *, **, *** = *P* < 0.05, < 0.01, < 0.001.
Biomass index = Length × width × number of leaves
Plastochron rate = Total number of leaves/age in weeks
N = Number of plants (for cotyledon length respectively: 55, 42, 27, and 22)

Table 4. Mean of various traits of *P. lanceolata* and *P. major* in gaps (treatments G10 and G5) and closed vegetation (treatments H15 and HN) measured on 20/7/1982. Plants are divided according their survival in the 20/7–20/9/1982 period (S = surviving; D = dead plants). Date of seedling emergence in weeks from 3/3/1982 onwards. Biomass index = Length × width × number of leaves. Plastochron rate = Total number of leaves/age in weeks.

| Character	*P. lanceolata*				*P. major*			
	Gap		Vegetation		Gap		Vegetation	
	S	D	S	D	S	D	S	D
Seedling emergence date	4.5	6.3	5.2	6.2	5.3	5.9	6.4	7.5
Cotyledon length (mm)	15.4	15.4	20.3	18.8	6.0	5.4	7.5	7.4
Leaf length (mm)	95.4	48.8	104.2	79.1	29.8	19.0	25.7	20.6
Length:width ratio	12.2	12.1	17.9	19.1	3.1	2.9	3.7	3.5
Number of leaves	3.1	2.3	2.6	2.4	4.0	3.1	3.5	3.2
Biomass index	2729	494	1963	1027	1344	535	983	461
Plastochron rate	0.20	0.17	0.18	0.18	0.28	0.23	0.26	0.26
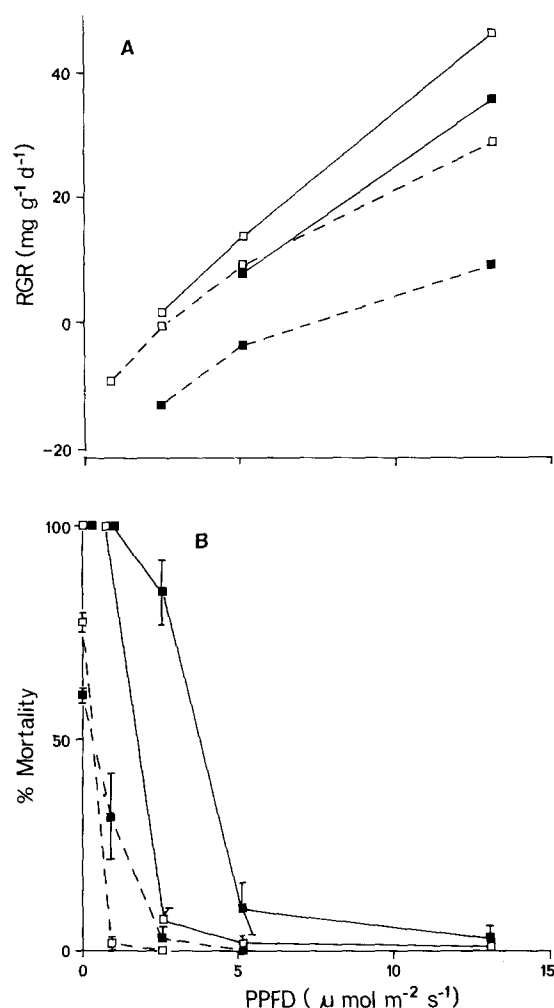
Fig. 3. A Relative growth rates (RGR) of seedlings of *P. lanceolata* (■) and *P. major* (□) at a range of low photosynthetic photon flux densities (PPFD). During the 21 days period between sowing and first harvest (—–—) and during the 28 days period between first and second harvest (——). RGR of the species at the same PPFD was significantly different (ANOVA) during the first period ($P<0.0001$), but not during the second period. **B** Mortality (mean and standard error) of seedlings of *P. lanceolata* and *P. major* at a range of low PPFD. Legend see **A**. Response of the species to PPFD was significantly different (ANOVA) at 49 days ($P<0.0001$), but not at 21 days after sowing

port. Hence, the ability of *P. lanceolata* to establish itself in a closed turf is not due to the tolerance of its seedling towards shade. On the contrary, the morphology of its seedlings which is an adaptation to the light gradient in grassland, is less suitable for the exploitation of low flux densities. Indications of a higher shade tolerance by *P. major* seedlings were also found in the field experiment. Many *P. major* plants survived in 1982 in the grass and these had emerged at about the same time as *P. lanceolata* seedlings, which succumbed later (Fig. 2). This was notwithstanding the fact that the smaller *P. major* seedlings experienced a lower PPFD in the grass than the taller *P. lanceolata* plants (c.f. Table 4).

Selection for early germination as found in the field experiment, occurred primarily via plant size. Quite unexpectedly, seed weight (as indicated by cotyledon length) played a less important role in seedling success. The selection for plant size can be explained by the existence of a dominance hierarchy which develops between seedlings for which an early start, via early germination, is of prime importance, especially in closed vegetation. Competition then leads to survival of the largest individuals (White and Harper 1970; Ross and Harper 1972; Fowler 1984). In this experiment competition will have been of both an intra- and interspecific nature. It seems likely that the plants competed mainly for light, as mortality and selection pressure are correlated with the light quantity (Fig. 1 A, B), but competition for nutrients will also have occurred (c.f. Blom 1979; Berendse 1983).

For the regeneration of grassland species from seed, natural gaps are supposed to be essential (Grubb 1982; Fenner 1978 a). Quite unexpectedly, in the field experiment *P. lanceolata* also established itself in undisturbed vegetation. This phenomenon can be explained by temporal differences in growth pattern, viz. early growth (germination) of *P. lanceolata* versus retarded growth of grasses. The earlier germination of *P. lanceolata* in contrast to *P. major* (Pons and Van der Toorn 1988), suits the strategy of a species of closed turf, as it increases its competitive ability. Early germination (in autumn or early spring), i.e. before the start of the main grass growth, is also found in other grassland species (viz. *Euphrasia stricta* Wolff ex J.F. Lehm. and *Gentianella germanica* (Willd.) Börner; During et al. 1985) and seems an important component of the strategy of these species.

The tendencies in the selection for early germination are similar in both species, although for *P. major* selection in closed grass is more severe. Similar quantitative differences in selection pressure are reported by Miller (1987) for an early old-field community. He found that the annual species *Ambrosia artemisiifolia*, *Chenopodium album*, and *Panicum capillare* were more suppressed by later emergence than the perennial species *Plantago lanceolata*, *Potentilla recta*, and *Trifolium repens* which could be related both to growth form (upright for the annuals and low lying for the perennials) and lifespan. Our data do not confirm this relationship but a rather good correspondence between Miller's and our data exists if the above-mentioned annuals are regarded as bare soil species and the perennials as species of a more closed vegetation. Although the latter are also found in open, waste places, they can persist – in contrast to the first – in older succession stages or in closed vegetation (cf Werner and Soule 1976; Bassett and Crompton 1975, 1978; Hitchcock et al. 1969; Gleason and Cronquist 1963).

In *P. major*, selection for early germination is low in open vegetation (Fig. 1 B). As the results of the field experiment also indicate that this species can only survive in open places, it seems unlikely that selection for early germination will be important in the natural habitats. In contrast to *P. major*, such selection seems important for *P. lanceolata* as competitive conditions are typical for hayfields. However, the significance of selection on germination date depends on the relative importance of gaps for seedling establishment.

In this study the term "selection" is used to describe the relationship between phenotype and fitness (as in Arnold and Wade 1984). An indication of the evolutionary significance of the demonstrated selection processes can be found in the corresponding differences between the two *Plantago* species when selection pressure and germination time in the natural habitat are compared: strong selection pressure in *P. lanceolata* may have led to early germination and less pressure in *P. major* to late germination. It is uncertain in how far these evolutionary processes are still active. If they are it means that some phenotypic variation in emergence time is (still) of genetic origin. The heritability of emergence time is unknown for both *Plantago* species and it can be expected that the influence of environmental factors such as depth of burial (c.f. Watkinson 1978) or soil topography, will be considerable. Differences in the time of germination between *P. lanceolata* populations with early germinating plants in the more competitive situation (Van Groenendael 1985) indeed indicate that variation in this trait is considerable. They also suggest that it is to some extent genetically determined. Similar differences (in seed dormancy) exist in *P. major* (Lotz, unpublished work). Furthermore, significant, although low, heritabilities are reported for other species (Arthur et al. 1973; Kalisz 1986).

In natural populations variation in selection pressure on the date of seedling emergence may occur on both a local and temporal scale (c.f. in *Collinsia verna*; Kalisz 1986). Our results indicate that the heterogeneity in vegetation structure is one of the factors involved in this phenomenon. Therefore, if variation in germination time in *P. lanceolata* is partly of genetic origin, it seems likely that under different competitive circumstances local and/or temporal shifts in mean emergence time are possible.

It can be concluded that *P. lanceolata*, in contrast to

P. major, can establish itself effectively among grass mainly because of its higher competitive ability. The capacity to form longer and more erect cotyledons and leaves is one of the traits contributing to the latter. The elongation of leaves is partly attained by a plastic response to the light climate which is more pronounced for *P. lanceolata*. Another trait contributing to the higher competitive ability of *P. lanceolata* is its earlier germination. The selective importance of this feature seems likely from our observations. All above-mentioned traits fit well in the general strategy expected for species of closed grassland versus bare soil (Grime and Jeffrey 1965; Fenner 1978a).

References

Arnold SJ, Wade MJ (1984) On the measurement of natural and sexual selection: theory. Evolution 38:709–719

Arthur AE, Gale JS, Lawrence KJ (1973) Variation in wild populations of *Papaver dubium*. VII Germination time. Heredity 30:189–197

Baskin JM, Baskin CC (1972) The influence of germination date on survival and seed production in a natural population of *Leavenworthia stylosa*. Am Midl Natur 88:318–323

Bassett IJ, Crompton CW (1975) The biology of Canadian weeds. 11. *Ambrosia artemisiifolia* L. and *A. psilostachya* DC. Can J Plant Sci 55:463–476

Bassett IJ, Crompton CW (1978) The biology of Canadian weeds. 32. *Chenopodium album* L. Can J Plant Sci 58:1061–1072

Berendse F (1983) Interspecific competition and niche differentiation between *Plantago lanceolata* and *Anthoxanthum odoratum* in a natural hayfield. J Ecol 71:379–390

Bishop YMM, Fienberg SE, Holland PW (1975) Discrete Multivariate Analysis: Theory and Practice. M.I.T. Press, Cambridge, USA

Blom CWPM (1978) Germination, seedling emergence and establishment of some *Plantago* species under laboratory and field conditions. Acta Bot Neerl 27:257–271

Blom CWPM (1979) Effects of trampling and soil compaction on the occurrence of some *Plantago* species in coastal sand dunes. Doct. thesis, Nijmegen, The Netherlands

Cook RE (1980) Germination and size-dependent mortality in *Viola blanda*. Oecologia (Berlin) 47:115–117

During HJ, Schenkeveld AJ, Verkaar HJ, Willems JH (1985) Demography of short-lived forbs in chalk grassland in relation to vegetation structure. In: White J (ed) The Population Structure of Vegetation. Dr W. Junk Publ., Dordrecht, pp 341–370

Endler JA (1986) Natural Selection in the Wild. Princeton Univ. Press, Princeton, N.J.

Falconer DS (1981) Introduction to Quantitative Genetics. 2nd Ed. Longman, London, UK

Fenner M (1978a) A comparison of the abilities of colonizers and closed-turf species to establish from seed in artificial swards. J Ecol 66:953–963

Fenner M (1978b) Susceptibility to shade in seedlings of colonizing and closed-turf species. The New Phytologist 81:739–744

Fowler N (1984) The role of germination date, spatial arrangement, and neighbourhood effects in competitive interactions in *Linum*. J Ecol 72:307–318

Gleason HA, Cronquist A (1963) Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Van Nostrand CY, Princeton, NJ

Grime JP, Jeffrey DW (1965) Seedling establishment in vertical gradients of sunlight. J Ecol 53:621–642

Grubb PJ (1982) Control of relative abundance in roadside *Arrhenatheretum*: results of a long-term garden experiment. J Ecol 70:845–861

Hitchcock CL, Cronquist A, Ownsbey M, Thompson JW (1969) Vascular Plants of the Pacific Northwest, Part 1–5. Univ. of Washington Press, Seattle

Hutchinson TC (1967) Comparative study of the ability of species to withstand prolonged periods of darkness. J Ecol 55:291–299

Kalisz S (1986) Variable selection on the timing of germination in *Collinsia verna* (*Scrophulariaceae*). Evolution 40:479–491

Lande R, Arnold SJ (1983) The measurement of selection on correlated characters. Evolution 37:1210–1226

Marks M, Prince S (1981) Influence of germination date on survival and fecundity in wild lettuce *Lactuca serriola*. Oikos 36:326–330

Miller TE (1987) Effects of emergence time on survival and growth in an early old-field plant community. Oecologia (Berlin) 72:272–278

Pons TL, Van der Toorn J (1988) Establishment of *Plantago lanceolata* L. and *Plantago major* L. among grass. I. Significance of light for germination. Oecologia (Berlin) 75:394–399

Poorter H, Lewis C (1986) Testing differences in relative growth rate: a method avoiding curve fitting and pairing. Physiologia Plantarum 67:223–226

Ross MA, Harper JL (1972) Occupation of biological space during seedling establishment. J Ecol 60:77–88

Sagar GR, Harper JL (1961) Controlled interference with natural populations of *Plantago lanceolata*, *P. major* and *P. media*. Weed Research 1:163–176

Sagar GR, Harper JL (1964) Biological Flora of the British Isles. *Plantago major* L., *P. media* L., and *P. lanceolata* L. J Ecol 52:189–221

Van der Toorn J, Ten Hove HJ (1982) On the ecology of *Cotula coronopifolia* L. and *Ranunculus sceleratus* L. II. Experiments on germination, seed longevity, and seedling survival. Oecologia Plantarum 3:409–418

Van Groenendael J (1985) Selection for different life histories in *Plantago lanceolata*. Doct. thesis, Wageningen, The Netherlands

Verkaar HJ, Schenkeveld AJ (1985) On the ecology of short-lived forbs in chalk grassland: seedling development under low photon flux density conditions. Flora 175:135–141

Watkinson AR (1978) The demography of a sand dune annual: *Vulpia fasciculata*. II. The dynamics of seed populations. J Ecol 66:35–44

Werner PA, Soule JD (1976) The biology of Canadian weeds. 18. *Potentilla recta* L., *P. norvegica* L., and *P. argentea* L. Can J Plant Sci 56:591–603

White J, Harper JL (1970) Correlated changes in plant size and number in plant populations. J Ecol 66:15–34