# Comparative demography of *Plantago*. I. Observations on eight populations of *Plantago lanceolata*

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## SUMMARY

The demography of *Plantago lanceolata* was studied in eight grassland habitats ranging from open unmanaged vegetations and pasture on dry sandy soil to hayfields with a high and dense vegetation on loam or clay soils. Data on density and survival of juvenile and adult plants and on aspects of natality were collected. The first two axes of a principal component analysis of these data represented 41% and 25%, respectively, of the total variance. Correlations of the axes with environmental factors of the respective habitats were calculated.

The first axis was primarily correlated with light transmission of the vegetation in summer. Thus, survival of juvenile and adult plants during the summer, and in general their density, was highest in open vegetations, while in dense vegetations survival in a severe winter and the number of seeds per plant were higher. Supporting evidence is given for the conclusion that the survival in summer, especially of young and small plants, is positively influenced by this factor. The most important (negative) contribution to the second axis comes from the survival in the second (mild) winter. This axis is significantly correlated with the organic matter and total nitrogen content and moisture content of the soil in winter. This correlation is probably caused by mortality due to water-saturation of the soil. During the period studied no adverse influence of drought in summer was found.

Key-words: demography, life-history traits, population ecology, *Plantago lanceolata*, shading, water-logging.

## INTRODUCTION

Demographic field studies are an important step in exploring the way in which plants function in relation to their environment. They can reveal which environmental factors are responsible for the variation in numbers and in which stages of the life cycle these factors exert their influence. Comparative studies on different species or on populations within one species can give the data that can be used as a starting-point for further studies, either on the ecophysiological aspects of the responses to the environment, or on the selection processes that have shaped the adaptation of the plants.

If the aim of the study is the comparison of different species, or, in general, the study of genetic variation between groups of plants, populations can be studied simultaneously in the same environment. The results then apply only to the specific environmental situation

in question. When the differences between species are great, this method can give distinct results as in the classic study by Sarukhán & Harper (1973) on species of *Ranunculus*. The results are less distinct, when the influence of the local environment dominates to a large extent the differences between species. When, on the other hand, the influence of the environment is the prime concern of the study, the performance of one species in different habitats can be compared. These approaches may be combined, following two or more species simultaneously in a range of habitats. In this case, however, the amount of work involved will limit the breadth or the detail of the study.

This study is part of a research project on the demographic, physiological and genetic properties of grassland plants in relation to the characteristics of their environment (Van der Aart 1985). The aim of the project is to investigate the factors that determine the distribution of the plants and their adaptation to the local situation in the field. The project concentrates on the five species of the genus *Plantago* that are indigenous in The Netherlands.

Four species, i.e. *P. coronopus* L., *P. major* L. ssp. *major*, *P. media* L. and *P. lanceolata* L., were studied simultaneously. Because these species have different habitat requirements (Haeck *et al.* 1982), a direct comparison of all species in one habitat could not be realized. The three first mentioned species have relatively narrow ecological amplitudes that do not show much overlap. *P. lanceolata*, however, has a wider ecological amplitude and occurs in most of the habitats in which the other species are found, as well as in habitats where the other four are not present. Therefore, *P. lanceolata* was used as a reference and the demographic properties of its populations were compared to those of the other *Plantago* species occurring in the same habitat. In this paper the performance of *P. lanceolata* in the contrasting habitats will be considered.

## METHODS

#### Collection of demographic data

Due to the large number of populations studied, not all life stages of the plants were studied. Observations on the survival of the seeds are not included. The plants were followed individually in permanent plots of  $0.3 \times 0.4$  m. As the aim of the study is the comparison between habitats, the permanent plots were chosen in a restricted and homogeneous part of the sites. The number of plots that varied between the sites because of differences in plant density are given in Table 1, together with the description of the habitats. The plants are classified into two groups according to age, namely those that germinated in the year of the census (juveniles) and those that survived at least one winter (adults). The presence of all rosettes (adults, juveniles, daughter rosettes) was recorded four times a year (end April–early May, end June–early July, end August and mid October) during 1978 and 1979 by drawing their position on a plastic overlay held by a frame placed over the plot. The survival of individual rosettes present in the autumn of 1979 was monitored in spring and autumn of later years.

The number of leaves per rosette in spring and data on flowering and seed production (in June) were also determined. The seeds were not harvested in the plots, but the length of the spikes was measured and the mean number of seeds per millimetre of spike was determined in 25 spikes collected in the neighbourhood of the plots.

## Description of the habitats

Table 1 shows a list of the populations studied, with a short description of the habitat and the values measured for a selection of environmental factors. In order to avoid

Table 1. Description of the habitats, with selected environmental factors

	Number of			Vegetation	Percentage	Soil mo percenti volu	isture age of me	Percentage	Total	Total	
Site	demographic plots	Soil type	Management	(cm)	light transmission	Summer	Winter	organic matter	murogen (p.p.m.)	pnospnorus (p.p.m.)	rotassium (meq/100 g)
1. Uddel	3	Sand	None, lightly trodden	œ	64	16	16	5-0	1470	193	0-13
2. Achterberg	10	Sand	Grazed by	6	54	28	33	5.9	1660	278	0.10
3. Achterberg havfield	15	Sand	Mown once (end June)	26	31	30	34	5-0	1440	235	0-13
4. Westervoort	80	Sand/clay	None, grazed by rabbits	39	12	25	38	9.9	2660	612	0-42
5. Pannerden	ø	Sandy loam	Lightly grazed by ponies	28	10	21	33	10-3	4190	878	0-52
6. Heteren havfield	80	Clay	Mown once (early July)	67	7	32	39	5.5	2310	907	0-60
7. Bruuk havfield	9	Peaty loam	Mown once	60	S	61	68	12-7	4250	578	0-25
8. Bruuk path	6	Peaty loam	Mown once	14	14	40	58	10.1	4100	444	0-25
	,		(August) trodden								

macroclimatic differences, e.g. severity of frost between coastal and inland sites, the populations were situated in a restricted inland area, approximately 100 km from the coast. Climatological differences between the years existed in the severity of the winter (Koninklijk Nederlands Meteorologisch Instituut, 1985). The winter of 1978/1979 was very cold, with a Hellmann-number of 205.7 (cumulated mean temperatures of all days with a mean temperature below 0°C in the period of 1 November–1 April), and the cold period lasted from mid December until mid February. The winter of 1979/1980 was normal with a Hellmann-number of 46.7. The summer periods of 1978 and 1979 had no outstanding characteristics; May 1980 was extremely dry.

The measurements of the soil chemical characteristics were carried out in bulk samples of three separate layers of 0-10 cm, 10-20 cm and 20-30 cm. The methods used are described by Troelstra *et al.* (1981). In Table 1 and in the calculations for Fig. 1 the data of the upper 10-cm layer were used for clarity and because the data for deeper layers showed a close correlation with those for the upper layer. Another reason is that the rooting depth of *Plantago lanceolata* is not very great, especially in the soils that are moderately compacted due to trampling (Blom 1979).

Vegetation height, light transmission and soil moisture were measured in June and in early July 1979 (before the hayfields were mown) during the period of maximum development of the vegetation. This coincides with the minimal values for light transmission and soil moisture. Soil moisture in the winter season of 1979–1980 was determined in February and late March–early April 1980. In Table 1 the means of the measurements taken in each demographic plot are given. Vegetation height was measured as the height above the ground of the centre of a styrofoam board ( $40 \times 40 \times 2$  cm, weight 45 g) placed on the vegetation, and the percentage light transmission by comparing the light at ground level to the light above the vegetation using three silicon photocells. Soil moisture (in the upper 5 cm) was determined using a capacitive method developed by the Technical and Physical Engineering Research Service, Wageningen (Ploegaert, 1978). The readings were converted to percentages of volume by simultaneous measurement of weight loss in a number of samples per soil type dried at 85°C.

## Statistical evaluation of the data

A considerable amount of data was obtained on natality and on survival of different life stages and in different periods; together this provided a basis for comparison of the demographic behaviour of the populations. The complexity of this dataset makes it difficult to decide which of the characteristics are the most important ones for the discrimination between the populations.

There were two further difficulties. The first was the statistical evaluation of differences between the values for a certain characteristic. In principle it should be possible to obtain an estimate of each of the demographic properties in each of the observation plots. The numbers of a certain category of plants (e.g. seedlings) in a plot were sometimes small or nil, so that no reliable estimate could be obtained for every plot and standard errors could not be calculated. It is not the significance of the difference between the values that is most interesting, however, but the relative position of the population with regard to the range of values for each demographic property. The second problem was that most or all of the characteristics are interrelated, which makes it impossible to single out without special statistical analysis those that contribute most to the differences between the populations.

Both problems can be solved by the use of principal component analysis, which requires the mean values per population for each variable. In the calculations the correlation

	Density of adults		Density of juveniles		Percentage flowering plants		Seeds per flowering plant		Percentage adults with daughter rosettes	
Population	1978	1979	1978	1979	1978	1979	1978	1979	1978	1979
Uddel	284	239	342	628	57	14	39	14	15	47
Achterberg pasture	105	167	174	118	19	21	53	54	8	10
Achterberg				. –					_	
hayfield	111	146	71	67	30	23	104	81	5	11
Westervoort	87	88	269	17	22	14	62	129	4	5
Pannerden	155	126	41	39	15	11	32	49	8	9
Heteren	59	64	99	54	177	25	229	166	7	16
Bruuk										
hayfield	311	173	290	96	1	24	7	38	1	35
Bruuk path	58	79	360	21	27	10	39	50	12	15

Table 2. Data on density (per m<sup>2</sup>) and parameters of natality in populations of Plantago lanceolata

matrix was used, which means that the contribution of each variable is independent of the range of its values. In this analysis the original (correlated) variables are objectively transformed to a new set of uncorrelated variables (principal component axes) that are linear combinations of the original measurements. The importance of the contribution of each of the original variables to the principal components can be evaluated as well as the proportion of the total variance accounted for by each of the principal components. Just as with the original variables, the correlations of the principal components with the environmental factors of the sites in which the populations are studied can be calculated (Williamson 1972).

## RESULTS

The demographic properties of the populations, as determined in 1978 and 1979, that were used in this analysis are listed in Tables 2 and 3. The density of adults and juveniles is given and three attributes describing natality, namely percentage of adults flowering, mean seed production per flowering plant and percentage of plants with daughter rosettes. Because the percentage of daughter rosettes was low in most cases, the mean number per plant is omitted. In the case of survival the data were calculated separately for juvenile and adult plants (genets), and for the summer (May–October) and winter (October–May) periods (Table 3).

The results of the principal component analysis of these data are given in Fig. 1A–C. The first principal component covers 41% of the total variance and the second 25%, while the remaining principal components explain 14% or less. Only the first two axes will be discussed. In Fig. 1A the correlations of the original characteristics with the principal components are shown, from which the relative contribution of these characteristics can be seen. In the first place it is evident that values for characteristics that correspond to each other are often situated close together in the figure. The two yearly values of the density of adults (a), the percentage of plants with daughter rosettes (c) and the number of seeds per

	SI	Perce urvival is	ntage n summ	er	Percentage survival in winter				
	ad	ults	juve	niles	adı	ults	juve	niles	
Population	1978	1979	1978	1979	1978/79	1979/80	1978/79	1979/80	
Uddel	89	92	71	70	64	91	29	76	
Achterberg pasture	94	83	66	36	91	93	64	63	
Achterberg									
hayfield	96	92	45	61	96	90	93	73	
Westervoort	77	80	24	15	78	79	39	57	
Pannerden	90	81	5	17	84	90	50	57	
Heteren	75	56	6	11	100	100	100	100	
Bruuk									
havfield	67	88	1	36	79	83	63	10	
Bruuk path	67	54	16	22	75	55	72	33	

#### Table 3. Data on survival in populations of *Plantago lanceolata*

flowering plant (h) are examples of this phenomenon. When, as for the components of survival, the location of the points differs between years and seasons, a correspondence is seen between the values for juveniles and adults.

The most important positive contributions to the first principal component are density of adults (a) and juveniles (b), survival in summer (d, e) and occurrence of daughter rosettes (c), while seed production per plant (h) and survival in the winter of 1978–1979 (g) show important negative contributions. The principal component 2 shows a strong negative correlation with survival in the winter of 1979–1980 (f) and weaker correlations with the percentage of flowering plants (i), seed production (h), and survival in the summer of 1978 (e) and in the winter of 1978–1979 (g).

For the interpretation of the different trends mentioned above, it is important to know the mean scores of the axes for each of the populations. These are given in Fig. 1B. From these values and the environmental data measured in the different sites, the correlation of the principal component axes with environmental values can be calculated as shown graphically in Fig. 1C. Due to the relatively low number of populations studied, the correlation coefficients have to be rather high to become significant (critical value at = 5%: r=0.71). This threshold is indicated on the axes in Fig. 1C. In the case of axis 1 only the correlation with light transmission is significant and in that of axis 2 the closely interrelated factors 'percentage of organic matter' and 'nitrogen-concentration' of the soil, and moisture in winter.

## DISCUSSION

#### Interpretation of the principal axes

Because correlations between the environmental factors are not eliminated in this analysis, it is necessary to look for supporting evidence to choose the factors that are most probably responsible for the variation between the populations. In the case of the



Fig. 1. Results of principal component analysis of demographic characteristics determined in eight populations of *Plantago lanceolata*. The first two principal component axes are shown. (A) Plot of 18 demographic characteristics; juv = juvenile plants, ad = adult plants. (a) Density of adults in spring; (b) density of juveniles in spring; (c) percentage of plants with daughter rosettes; (d) survival during the summer of 1979; (e) survival during the summer of 1978; (f) survival during the winter of 1979/1980; (g) survival during the winter of 1978/1979; (h) number of seeds per flowering plant; (i) percentage of flowering plants. (B) Scores of the populations on the principal component axes. The numbers of the populations correspond with those in Table 1. (C) Plot of correlation coefficients of habitat factors with the populations correspond with those in Table 1. (C) Plot of level (June–early July); VH vegetation height (June–early July). Soil factors: (OM) organic matter content; (N) total nitrogen concentration; (MS) moisture in summer (percentage of soil volume in June–early July); (MW) moisture in winter (percentage of soil volume in February–early April 1980); (P) total phosphorus concentration; (K) potassium concentration; pH = pH–KCl; all soil factors are given for the top 10 cm of the soil. The threshold for significance (P = 0.05) is given as a transverse line on the axes.



Fig. 2. Survival of *Plantago lanceolata* plants of different size in relation to the light transmission in the vegetation. ( $\bigcirc$ ) 1978, ( $\bigcirc$ ) 1979.

demographic characteristics that have a large contribution to axis 1, it is plausible that differences in light transmission had the greatest influence. In particular, the survival of plants during the summer season has a high positive correlation with light transmission (Fig. 1A and C). In Fig. 2 the plants have been divided in a different way from that in Fig. 1A. The data of Fig. 2A, concerning the seedlings, are the same as used in the category of juveniles in Fig. 1A. In this category a rather steep regression can be seen. The plants without cotyledons, mainly adults, have been split up into those with between one and three and those with four leaves and more during the May census. Clearly, regression becomes less important as the plant size increases. In the plants with four leaves or more it is not significant. For plants within one population, leaf length is correlated to the number of leaves per rosette (J. Haeck, unpublished observations). Because in dense and high vegetation the leaves grow vertically, shorter leaves will catch less light than longer ones. This is probably the reason for the lower survival rate of small plants as compared to that of larger plants. Mortality in the denser vegetations was almost entirely concentrated in the period between the April–May census and June–early July census, the period of lowest light transmission. This is in agreement with the hypothesis that light is the principal factor.

An increase in the density of the above-ground vegetation will coincide with an increase in the root biomass. Competition for nutrients and moisture might also be an important cause of mortality. The correlation of soil nutrient concentration (phosphorus and potassium) with axis 1, however, is negative (r = -0.65; P = 0.08). This points to a relatively low survival in summer on the richer soils with a dense vegetation and a high survival on the poor soils with open vegetation. Although this does not rule out the possibility that underground competition for nutrients plays a role, it is more probable that light is the most important factor. For similar reasons competition for water is probably not a major factor in the period studied, soil moisture being negatively correlated with survival.

The correlations of the other demographic characteristics with axis 1 can all be, at least partly, explained by the open-to-dense-vegetation gradient. It is plausible that juvenile density is higher in open vegetation because of better circumstances for germination and establishment. Adult density is largely dependent on recruitment and survival in different seasons. The negative correlation of openness with survival in the severe winter of 1978– 1979 may have been caused by the lack of cover in the open vegetation (cf. low survival in Uddel, Table 2). The greater seed production of plants in dense vegetation, especially Heteren, was also found in a transplantation experiment by J. Van der Toorn & P.H. Van Tienderen (personal communication). Potential seed production, however, as found in a common garden experiment (Van der Toorn & Ten Hove 1982), is higher in plants that originate from open, grazed vegetation types. Thus the actual seed production is largely determined by grazing. The higher percentage of plants with daughter rosettes in the open vegetation may be caused partly by damage from grazing or trampling and, in the Uddel population in 1979, by frost damage.

The environmental basis of the correlations of demographic characteristics with axis 2 is less clear than that with axis 1. Nearly all of the demographic characteristics, except those concerning the density of rosettes, show some negative correlation with axis 2, of which survival in the winter of 1979–1980 is the most prominent. Inspection of the original demographic data (Tables 2 and 3) gives some indication for clues, considering that all variables are interrelated and that some of the relations may be secondary. The negative contribution to axis 2 of survival in the second winter is caused primarily by the low survival in the Bruuk hayfield and Bruuk path sites (sites 7 and 8 respectively in Fig. 1B and Table 3), which score relatively high on the second axis. The soil of both sites is loam with some peat, with a relatively high concentration of organic matter and total nitrogen (Table 1). The correlation of moisture in the winter of 1980 with this axis is also primarily due to the high values for the two Bruuk sites.

Thus, although the correlation of axis 2 is higher with the percentage of organic matter and nitrogen, it is more probable that soil moisture is the primary factor, the more so, because in winter the mineralization of nitrogen in the soil and the uptake of nutrients by the plant will be lower than in the warmer seasons. K. Dilz (personal communication) has found that grasses that grow at high nitrogen levels are susceptible to frost. This is an unlikely explanation for the high mortality in this case because even the highest nitrogen concentrations are not exceptional and the winter of 1979–1980 was not severe. Based on known ranges of pore volumes of different soil types it was calculated that the soil at these sites was probably water-saturated. This makes it a plausible hypothesis that the high mortality was connected with an excess of water or a factor correlated with this (e.g. lack of oxygen for root respiration).

#### Comparison with other studies

Cook (1979), in a treatment of juvenile mortality in plants, concluded that herbivores, pathogens and drought stress are the most important causes of mortality. In other case studies drought is also found to be an important factor. In The Netherlands this was found by De Jong & Klinkhamer (1984) for biennials in coastal dunes and by Schenkeveld & Verkaar (1984) in the early seedling stage of various plants in chalk grassland.

In addition, in *P. coronopus* (Waite 1984) and *P. lanceolata* (Van Groenendael 1985) drought has been mentioned as an important mortality factor of both juvenile and adult plants. Van Groenendael found that during an extremely dry period in May and early June 1980, the survival of adult plants in an open coastal dune grassland was less than 10%. Although wilting of the plants was observed in some of our habitats during the same period, survival of adult plants was not exceptionally low. In the driest habitat (Uddel) the survival was 68%, while in the other habitats it was between 75% and 92%. The finer and somewhat compacted sand in the Uddel site evidently offered better survival circumstances than the coarse dune sand in the situation studied by Van Groenendael. A low survival rate in summer as a result of drought seems to be an uncommon phenomenon in *P. lanceolata*, presumably depending on the local soil characteristics.

A high winter mortality in a fen habitat, especially of juveniles, was also found by Van Groenendael (1985) in the respectively normal and mild winters of 1979/1980 and 1980/ 1981. Blacquière (1988) found that *P. lanceolata* is able to adapt to a high soil water table by a relatively low but significant aerenchyma formation in the roots. Formation of new roots with a higher porosity as a response to inundation was found by Schat (1982) to occur in *Plantago coronopus*. The latter species survived flooding more effectively in the presence than in the absence of *Juncus maritimus*, which has highly aerenchymatous roots.

Bakker et al. (1980), Verkaar & Schenkeveld (1984) and Van der Toorn & Pons (1988) have demonstrated the importance of the density of the vegetation and low light levels for mortality of seedlings of grassland plants. According to Grime & Jeffrey (1965), Hutchinson (1967) and Verkaar & Schenkeveld (1984), between species differences in seed reserve are positively correlated with the ability of seedlings to survive periods of shading. The much greater mean seed weight of *P. lanceolata* populations from dense habitats as compared to open habitats, which is partly genetically determined (Van der Toorn & Ten Hove 1982, Wolff 1988), might influence survival of seedlings in this way. In addition, the greater mean length of coleoptiles and primary leaves of seedlings from large seeds could have a positive effect on survival in dense vegetation (Van Groenendael 1985).

It cannot be concluded how far the continued existence of the populations and the differences in the life history in the large range of habitats are the result of plastic response or of adaptation of the plants to the local environment. Blom (1983) found that striking differences in the life history of two populations of *Plantago maritima* were based on

plastic reactions. In the case of *Plantago lanceolata*, however, Van der Toorn & Ten Hove (1982), Van Groenendael (1985) and Wolff (1988) showed that differences in morphology and life history are partly genetically based and that selection is important for the maintenance of this variation between populations.

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