LIFE HISTORY CHARACTERISTICS
OF TWO ECOTYPES
OF PLANTAGO LANCEOLATA L.

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SUMMARY

The life history of two populations of *Plantago lanceolata* L. from two different habitats is described, using standard demographical techniques. The first habitat is an open dune grassland on poor sandy substratum and grazed as a commonage for centuries. The vegetation occasionally suffers from drought. The second habitat is a closed hay meadow on organic substratum that is permanently waterlogged and mown once a year in July. The plantains in the dry site form small flat rosettes with many leaves and side rosettes. Small seeds are produced from many globular inflorescences on short ascending stalks late in the season (known as subvar. *sphaerostachya* f. *minor*). The plaintains in the wet site form few tall erect leaves and no side rosettes. Big seeds are produced from few long inflorescences on long stalks in the early season (known as subvar. *latifolia*). Seeds from the dry population show innate dormancy that shifts the main germination period of this population towards spring. The seeds require light and high temperatures for germination and form an appreciable seedbank. Seeds from the wet population show little dormancy and germinate readily in autumn at low temperatures and light intensities without forming a seedbank. Juveniles and adults share more or less equal risks in the dry site. Rosettes are short-lived and can flower in the second season even at small sizes. Seeds are produced at considerable costs. Juveniles are clearly more at risk in the wet site, where it takes several years to first flowering. Adults are long-lived and flower repeatedly, producing seeds at low costs. The results are discussed in connection with theoretical predictions from current life history theories.

1. INTRODUCTION

Since Turesson's important work on intraspecific variation in plants in relation to habitat characteristics (e.g. TURESSON 1922a, b, 1925)a whole field of research has developed, which is nowadays usually referred to as genecology (HESLOP-HARRISON 1964), but which has its roots much earlier, going back to the seventeenth and eighteenth century (BRIGGS & WALTERS 1984; LANGLET 1971).

It is not suprising that such a successfull approach has also been advocated in a related but much younger field of research: The evolution of life history tactics (STEARNS 1976; ETGES 1982; BARBAULT 1984). A tactic has been defined as a complex adaptation 'as a set of coadapted traits designed, by natural selection, to solve particular ecological problems' (STEARNS 1976). In the case of life history tactics, life history traits are involved. e.g. age- and size-dependent survival, reproduction, longevity and time to first reproduction. The emphasis on

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life history traits stems from the fact that it is through differential reproduction and survival that evolution takes place. The knowledge of any co-adapted pattern in life history traits would therefore improve our understanding of evolution. This interest has yielded a wealth of theories that has grown and is still growing without much empirical testing. According to STEARNS (1976), there exist two main life history theories, that produce almost completely contrasting predictions of life history traits in 'stable' versus 'unstable' environments. These two theories are labelled r- and K-selection theory and theory of bet-hedging. A set of data to test the theory with, again according to STEARNS (1976) should fulfil three criteria. These data should describe (1) the life history in demographical terms with special attention given to reproductive effort, as this is a central tenet of the theory. (2) The tests on the differences in life history tactics should preferably be performed using populations of different ecotypes of the same species and, lastly (3) the populations must show differences in density-dependence in the field, as this is another central tenet in these theories.

Notwithstanding the fact that some studies of life history tactics have used intraspecific variation in plants (BÖCHER 1949; references in STEARNS 1977; LAW et al. 1977; CASWELL & WERNER 1978; VAN DER VEGTE 1978; WATKINSON & HARPER 1978; ANTONOVICX & PRIMACK 1982; BLOM 1983), these studies remain relatively few. The reason could be that in using plants, some modifications have to be applied to Stearns' original scheme. It is not until recently (HARPER 1977) that population biology of plants has grown to full maturity. This is, among other reasons, due to problems in defining a plant individual. Vegetative spread is quite common and this complicates demographic counting of individuals. By recognizing the plant as a modular unit (HARPER & WHITE 1974; WHITE 1979) this problem can be solved, but it is this same modular construction that poses great problems in defining reproductive effort (WATSON 1984; WATSON & CASPER 1984).

Another problem is that it is difficult to define precisely what goes on between plant individuals that grow together and even more difficult to discriminate between the effects of the own or of a different species. Therefore density dependence is usually equated with competitive ability, regardless of the nature of the competitors but, as pointed out by BOYCE (1984), these two need not be identical and this could affect the comparison between theory and empirical data. Nevertheless, it is the purpose of this paper to compare two ecotypes of *Plantago lanceolata,* one from a 'stable' and the other from an 'unstable' habitat. Demographical data, collected over a three year period, will be used to test the following hypotheses, modified from STEARNS (1976):

(1) Is juvenile mortality most affected in unstable environments as predicted by the theory of bet-hedging or is adult mortality most affected as predicted by the r- and K- selection theory?

(2) Is there late first reproduction in unstable environments as predicted by the theory of bet-hedging or early first reproduction as predicted by the r- and K-selection theory?

(3) Is there a tendency towards polycarpy in unstable environments as predicted

by the theory of bet-hedging or a tendency towards monocarpy as predicted by the r- and K- selection theory?

(4) Are there few (big) seeds in a seedcrop in unstable environments as predicted by the theory of bet-hedging or many (small) seeds as predicted by the r- and K- selection theory?

(5) Is there a relatively small reproductive effort in unstable environments as predicted by the theory of bet-hedging or is there a relatively large reproductive effort as predicted by the r- and K- selection theory?

(6) Is there long adult longevity in unstable environments as predicted by the bet-hedging theory or short adult longevity as predicted by the r- and K- selection theory?

2. MATERIAL AND METHODS

2.1. Plant material
Plantago lanceolata is a short-lived perennial herb, forming a rosette and producing long stalked inflorescences from axillary meristems that can also give rise to side rosettes (SAGAR & HARPER 1964; CAVERS *et al.* 1980). The flowers are born in spikes, they are self-incompatible and each flower contains two ovules. It produces relatively large, smooth, oblong seeds about 3 mm long, weighing about 2 mg each, with a mucilaginous testa. The seeds are reported to germinate readily in light and in the dark at temperatures ranging from 10°–30°C, with an optimum around 23°C and to be stimulated by fluctuating temperatures (STEINBAUER & GRIGSBY 1957; BLOM 1978; GRIME *et al.* 1981). POVILAITIS (1956) and MORTIMER (1974) mention primary or innate dormancy and STEINBAUER & GRIGSBY (1957) describe a reduced germination in the dark that can be relieved by 0.2% potassium nitrate solution but the reverse, stimulation of germination in the dark, is reported by SAGAR & HARPER (1960) and BLOM (1978).

After germination *Plantago lanceolata* can grow quite quickly (MILTON 1943) but usually is found to possess a moderate relative growth rate (GRIME 1979). Although plants may flower within six weeks after sowing in the greenhouse or experimental garden, it usually takes individuals more than one season in the field. Flowering is induced by long day conditions (SNYDER 1948). During growth a variable number of side rosettes is formed, which increases the number of axillary meristems from which inflorescences may originate (SOEKARJO 1980; VAN GROENENDAEL 1985a), thereby increasing the reproductive output. It is known to adapt to all kinds of circumstances partly by phenotypic plasticity (ANTONOVICS & PRIMACK 1982; VAN GROENENDAEL 1985b) and partly by forming distinct ecotypes (BÖCHER 1943; PRIMACK, 1976; TERAMURA 1978; WARWICK & BRIGGS 1979; SLIM & VAN DER TOORN 1983) even at very short distances (FOWLER & ANTONOVICS 1981).

2.2. Site description
Plantago lanceolata itself grows in the Netherlands in a variety of mainly grassland habitats (WESTHOFF & DEN HELD 1969; HAECK *et al.* 1982), tolerating a
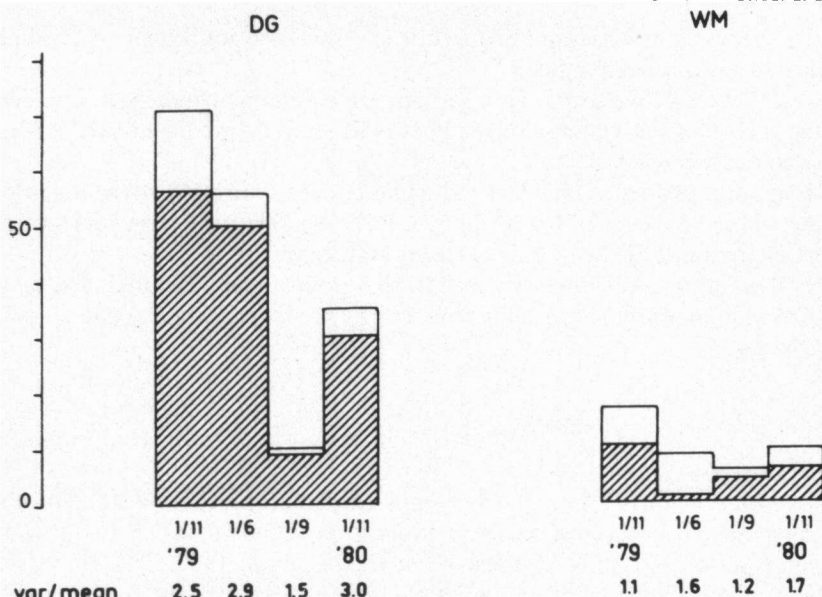
Figure 1. Number of seeds in the soil for *Plantago lanceolata* in a dry dune grassland (DG) and a wet meadow (WM) at 4 moments in the year, based on 50 soil samples each. The clustering of seeds in the samples is indicated by the variance over mean ratio. The number of seeds present in the top layer (0–1 cm) is indicated by shading. The remaining seeds were found between 1 and 10 cm.

wide range of microclimatological (STOUTJESDIJK 1981) and edaphic (TROELSTRA *et al*. 1981) conditions. Two contrasting habitats were selected differing in degree of stability to allow straight-forward interpretation of differences in life cycle characteristics afterwards. The first study site was located on the island of Goeree in a dry dune grassland which had been in use as a commonage and grazed by cattle and horses for at least three centuries (NOË & BLOM 1982). The grassland consists of a complex of dry dunes and wet dune slacks, with *Plantago lanceolata* more or less abundant in an intermediate situation. According to the classification of dutch vegetationtypes (WESTHOFF & DEN HELD 1969), this vegetation belongs to the class of the dry grasslands. As a result of the gradient on the slopes of the dunes (BLOM *et al.* 1979), it is intermediate between two alliances, Thero-Airion and Galio-Koelerion. It is an open grass sward of low productivity on leached, formerly calcareous sandy substratum, which dries out easily. Consequently the vegetation suffers from unpredictable and sometimes catastrophic summer droughts. Winter annuals and deep rooting forbs are dominant. Many ruderals in low densities indicate the impact of trampling and other types of disturbances associated with grazing. Rosettes of *Plantago lanceolata* in this vegetation are small and prostrate and posses many leaves and ascending inflorescences with small roundish spikes, a form known as subvar. *sphaerostachya* Mert. et Koch f. *minor* (see PILGER 1937). They form more or less clearly-defined patches, mainly because of the many side rosettes formed in this popu-
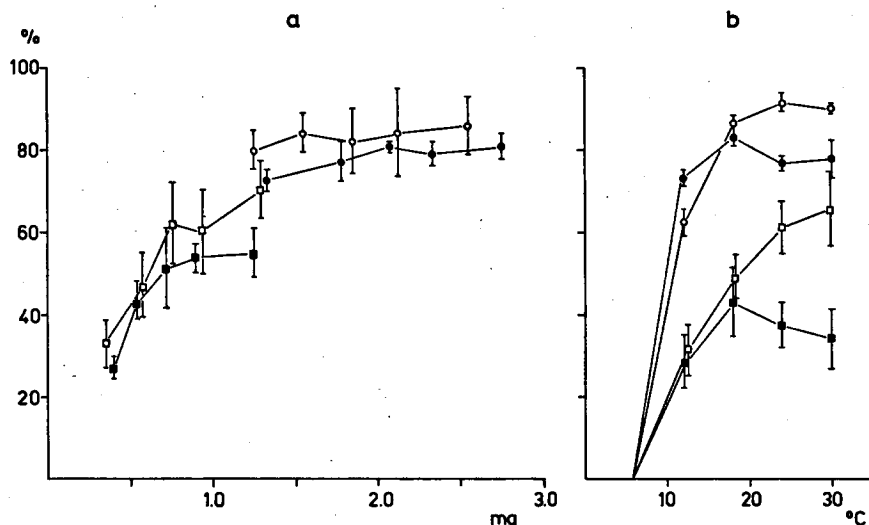
Figure 2. Percentage germination after six weeks, of vital, one year old seeds of two populations of *Plantago lanceolata* as a function of seedweight, tested at 21 °C (a) or as a function of temperature (b). The population from the dry dune grassland is represented by squares, the population from the wet meadow by circles. Open symbols refer to tests conducted in light, closed symbols to tests in dark. Bars indicate the standard error.

lation. The plants flower late in the season, from July to September.

The second study site is a wet hayfield on the island of Voorne, which is mown once a year in the beginning of July. This meadow has been used for generations for hay-making. It is situated in an old medieval river bed, now completely filled in. The vegetation in which *Plantago lanceolata* is found belongs to the class of wet grasslands and more specifically to the alliance Calthion palustris. This type of vegetation forms a closed, tall turf of intermediate productivity on completely organic substratum, with the watertable constantly at or at most a few centimeters below the surface. The vegetation is rich in species, dominated by sedges and grasses and with many forbs. The rosettes of plaintain have long erect leaves and erect inflorescences with elongated spikes on long scapes. This form is known as subvar. *latifolia* Wimm. et Grab. (see PILGER 1937). Side rosettes are formed only rarily and the plants are distributed more or less randomly over a wide zone of the marsh.

2.3. Demography
In both sites a series of three quadrats was set out, each of 0.125 m² and marked with fixed cornerpoles over which a transparant drawing table could be fitted. The quadrats were placed close to each other in the centre of the same population, where the density of plaintains was greatest. Apart from winter time, all rosettes were recorded onto plastic sheets every six weeks. Each rosette was given a fixed number and its fate was followed over three seasons: 1979, 1980 and
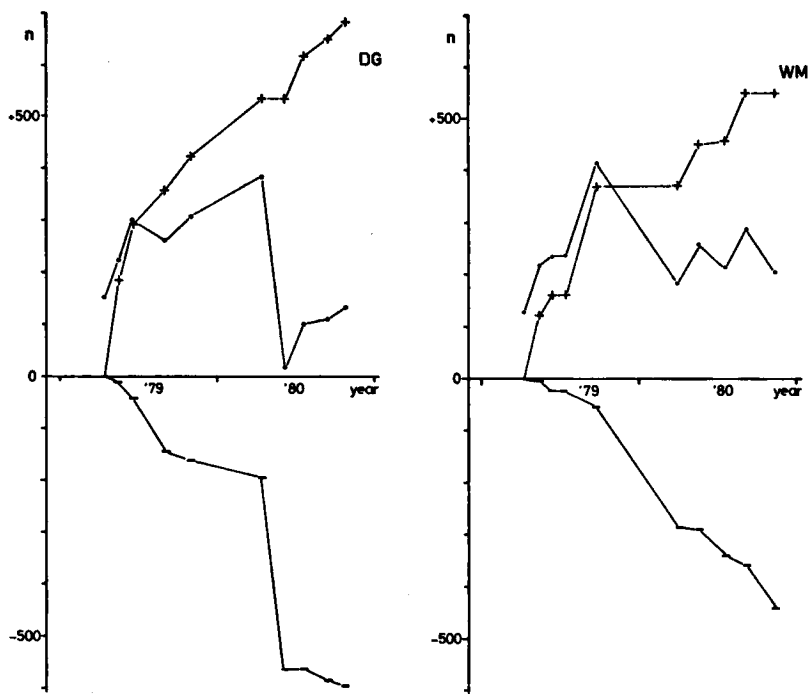
Figure 3. Total number of rosettes of *Plantago lanceolata* over time present in 0.375 m² in a dry dune grassland (DG) and in a wet meadow (WM). Cumulative numbers of rosettes that were born (+) and that died (−) are presented as well.

1981 respectively. The following data were obtained: number of leaves, length of longest leave, number of ears, length of longest scape, the length of the spike attached to the longest scape, its phase of flowering and herbivore damage to leaves and spikes. Lastly, mode of birth of the rosette was registered, either as a side rosette – and from which parent rosette – or as a seedling. In the case of seedlings the length of the cotyledons was measured as well.

Four times, at three-monthly intervals during 1979, 50 soil cores of 10 cm length and 3 cm diameter were taken randomly from a 10 cm grid with 200 positions, overlying the same population which was recorded demographically. The cores were divided into four layers: 0–1 cm; 1–4 cm; 4–7 cm and 7–10 cm. These were spread onto wet sterile sand in the greenhouse and plantain seedlings which emerged were counted and removed. Because only few seedlings emerged from the three deeper layers, these were taken together in the analysis. After three months the soil was sieved to retrieve any remaining seeds. These were dissected and tested for viability using vital staining with 0.1% tetrazoliumchloride solution at room temperature for six hours. In this way informations was obtained on size and seasonality of the seedbank.

With respect to the contrasting information in the literature about germination requirements, tests were conducted during the winter of 1980. Three petri
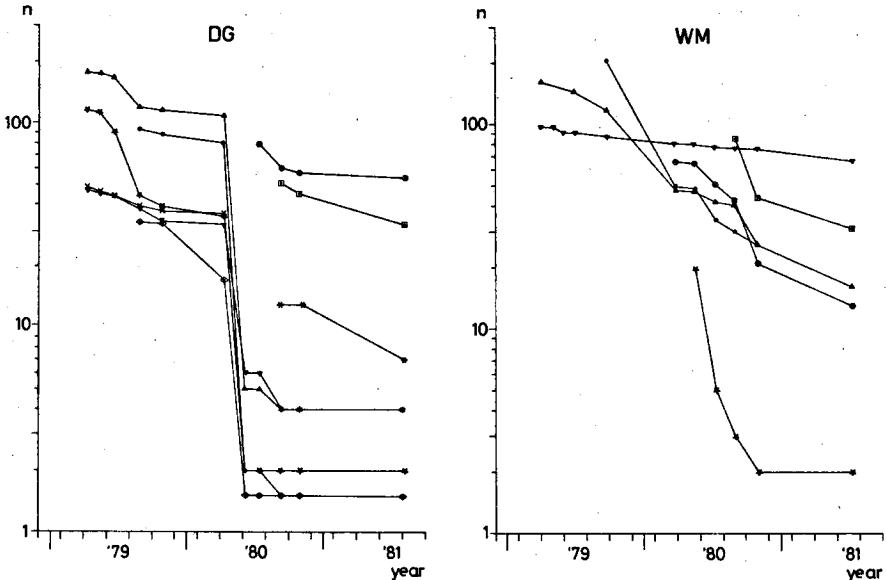
Figure 4. Survivorship curves for various cohorts of *Plantago lanceolata* from a dry dune grassland (DG) or from a wet meadow (WM). Symbols are as follows: ▲ spring cohort of seedlings 1979; ● autumn cohort of seedlings 1979; ★ spring cohort of side rosettes 1979; ◈ autumn cohort of side rosettes 1979; ▼ rosettes present in spring 1979; × genets present in spring 1979; ◉ spring cohort of seedlings 1980; ◙ autumn cohort of seedlings 1980; ✳ spring cohort of side rosettes 1980.

dishes were used per treatment, each containing 50 seeds on wet filter-paper. Seeds were collected in bulk in both habitats during 1979 and stored dry at 4 °C before using. The petri dishes were placed in incubators and the germinated seeds were removed at regular intervals. When no further germination was observed, the remaining seeds were tested for viability, using vital staining like before. Germination is expressed as a percentage of the vital seeds. The following factors were tested: constant temperatures (6 °C, 12 °C, 18 °C, 24 °C and 30 °C) in light 16 hrs per day, and in darkness; age in weeks (6 and 12 weeks, respectively) at 24 °C in light and finally seed size, distributing the seeds by hand over 5 size categories, each category with about equal numbers, again at 24 °C in light. Petri dishes used for the dark treatment were filled with seeds, wetted and immediately wrapped in aluminium foil. Twelve replicates were used in this case, so that germination could be followed over 4 time intervals of 10 days each.

Because of the relatively long interval of 6 weeks between the recordings in the permanent quadrats, more precise data were collected during the flowering season. About 30 adult rosettes were selected just outside the quadrats. The leaves and ears in these rosettes were marked with paint, using a technique described by BLOM & VAN HEESWIJK (1984). The fate of the leaves and ears was recorded at weekly intervals during the flowering season in 1980. Thus, turnover rates were obtained for leaves and ears with which the demographic data could be complemented.

Table 1. Size dependent life history traits for a population of *Plantago lanceolata* from a dry dune grassland measured in the season of 1979. Size is based on number of leaves × length of longest leaf in mm and divided in five categories of increasing magnitude (50, 100, 200, 400 and > 400). Symbols are as follows: nr number of main rosettes; fr flowering rosettes; ne/r number of ears per rosette; ns/e number of seeds per ear;ns/r number of seeds per rosette; de damaged ears; dr damaged rosettes; su rosettes surviving until the next summer; rz rosettes with side rosettes; nz/r number of side rosettes per rosette; nz number of side rosettes that survived until the flowering period; fz flowering side rosettes.

size	nr	% fr	ne/r	ns/e	ns/r	% de	% dr	% su	% rz	nz/r	nz	% fz
1	67	0	0	–	–	–	0	0	5	2.7	4	0
2	70	3	1.5	13	20	0	14	1	6	3.3	8	25
3	84	21	1.8	16	29	12	19	8	8	3.1	14	43
4	44	55	3.2	20	62	19	23	11	43	4.0	17	65
5	2	(100)	3.0	26	77	18	50	0	0	0	1	(100)
mean		17	2.7	19	42	18	14	5	12	3.6		46

3. RESULTS AND DISCUSSION

3.1. Seedbank and germination

Individuals of *Plantago lancolata* are considered independent as a seed in the soil or on the soil surface, together forming the seedbank. In the dry dunes there are more seeds in the seedbank than in the wet meadow and the seeds are more concentrated in the top layer of the hard sandy soil. Of all seeds, 79%, 90%, 87% and 85% respectively are found in the uppermost cm of the soil profile at the four sampling dates (*fig. 1*). In the marshy soil of the meadow the seeds are buried deeper in the soft substrate (52%, 17%, 75% and 57% respectively in the top cm of the soil profile) and show less variation in numbers over time. There is also a less pronounced pattern in space, as indicated by the variance over mean ratio (values closer to unity). In the dry dunes the spatial distribution is more clustered as one would expect with a clustered distribution of adult plants and a limited seed dispersal.

The differences in the extent and persistence of the seedbank can be related to differences in germination requirements as observed in laboratory tests. In general, seeds from the dry site germinated less easily and showed a higher light requirement for germination than seeds from the wet meadow population. The capacity to germinate reduces with decreasing seed size in the dry dunes while there is no such effect in the bigger seeds from the wet meadow (*fig. 2a*). The germination response to temperature is also clearly different. Seeds from the meadow population germinate better at lower temperatures and have a lower optimum temperature than seeds from the dune population (*fig. 2b*). Age has a more pronounced effect in the dry population. Six week old seeds from this population show a stronger innate dormancy than six week old seeds from the wet population (percentage germination 30 ± 10 and 54 ± 7 for wet and dry population, respectively). After twelve weeks this innate dormancy is relieved (percentage germination 75 ± 8 for wet and dry population.

Table 2. Size dependent life history traits for a population of *Plantago lanceolata* from a wet hay meadow measured in the season of 1979. Size is based on number of leaves × length of longest leaf in mm and divided in five categories of increasing magnitude (150, 300, 600, 1200 and > 1200). Symbols as in *table 1*.

size	nr	% fr	ne/r	ns/e	ns/r	% de	% dr	% su
1	65	0	0	–	–	–	3	22
2	69	0	0	–	–	–	2	25
3	35	11	1.8	35	62	0	2	57
4	47	32	1.7	36	56	52	0	83
5	27	82	1.9	51	94	36	0	93
mean		17	1.7	44	76	38	2	53

Field observations support the germination characteristics found in the laboratory. In the wet meadow, conditions are always cooler with little light penetrating to the soil surface (STOUTJESDIJK 1981), so that germination might be possible at low temperatures and under low light intensities. There is little innate dormancy so that germination can take place in autumn with a second possibility in early spring when the vegetation is relatively open. This is in agreement with the actual pattern in the field (see *fig. 3*). There is also very little enforced dormancy and this results in low numbers of seeds in the seedbank. The large number of seeds in the seedbank in the dry dune grassland is the result of the opposite conditions. There is innate dormancy, shifting the main germination towards the spring and enforced dormancy occurs as a result of light and temperature requirements, producing a considerable seedbank.

3.2. Population dynamics

The overall population dynamics of both ecotypes, presented as the total number of individuals over time, together with the cumulative number of births and deaths, is given in *fig. 3*. In the dry dune grassland the greatest mortality is found in summer as a result of catastrophic droughts, while in the wet meadow mortality is greatest in winter. In both sites there are two germination flushes, but the main period of germination is at spring in the dry site and at autumn at the wet site.

More insight can be obtained by inspecting the age dependence of birth and death processes. The fate of the various age categories is drawn as cohort survivorship curves in *fig. 4*. Juveniles carry the greatest risk with greatest mortality over winter, especially for those plants that have germinated in autumn. Their half-life is about four months. For the spring cohort of seedlings this is about six months, whereas adults have an estimated half-life of about 49 months. After about two years the plants reach a very stable survivorship, but it takes at least three years before they can flower. How age affects the reproductive output will be discussed below.

At the dry site juveniles and adults share the risks more or less equally. Estimated half-life for adults is between 19 and 21 months, excluding the effects

Table 3. Morphological aspects of seed production measured in flowering rosettes of two popula-
tions of *Plantago lanceolata*, from a dry grassland and a wet meadow, respectively.

	dry grassland			wet meadow		
	n	mean	CV%	n	mean	CV%
Number of ears/rosette	53	3.8	45	35	1.7	47
Number of ears/genet	32	9.2	69	35	1.8	47
Length of spike mm	53	7.3	31	35	17.1	34
Flowers/spike	30	15	53	30	63	64
Seeds/spike	30	16	75	30	57	53
Weight/seed mg	30	0.7	75	30	1.9	39

Table 4. Correlation coefficients between various traits related to seed production in two populations
of *Plantago lanceolata* for a dry dune grassland and a wet meadow, respectively. Reproductive effort
is calculated as mg seed-weight produced per cm^2 of leaf area. Growth is calculated between the
census directly preceding the onset of flowering and the moment when most seeds were ripe and
based on non-destructive estimates of biomass (number of leaves × length of longest leaf).

	dry grassland			wet meadow		
	n	r	p	n	r	p
Number of leaves × number of ears	53	0.395	<0.01	35	0.330	<0.05
Seed-weight × leaf area	53	0.602	<0.001	35	0.330	<0.01
Seed-weight × reproductive effort	53	0.514	<0.001	35	0.095	ns
Length of spike × seeds/spike	30	0.716	<0.001	30	0.903	<0.001
Seed-weight × seeds/mm spike	30	−0.449	<0.01	30	−0.214	ns
Growth × reproductive effort	18	−0.561	<0.05	46	−0.489	<0.001

of the catastrophic drought. For juveniles half-life is about 18 months but the
extremes are more pronounced, ranging from 12 to 24 months. After about six
months juveniles reach a stable survivorship. Plants can flower the second season
after germination. The cohort carrying the greatest risks is that of side rosettes,
but nevertheless they have a pronounced effect on genet survival. Half-life of
genets is about 31 months, which is much better than the ramet half-life of 20
months. Given the catastrophic drought, the effect of age on reproductive effort
could not be established.

    Although it is clear that there are important differences in age-dependent sur-
vival and time to adulthood, these differences have their greatest effect in early
life. After that period, size could be a more important criterium in the demogra-
phy of these plants (see also WERNER & CASWELL 1977). The effect of size on
seed production, survival, side rosette formation and herbivore damage is given
in *table 1* and *2*). Reproduction starts at smaller sizes in the dry population,
more plants per category do flower and there is a stronger relation between
size and seed production. Once committed to flowering, plants in the wet site
produce a rather constant number of ears. The seed production is not so clearly

dependent on size. Side rosettes, formed in the dry site, also show a clear size dependence. Those that survive until the summer have a greater chance of flowering than normal rosettes and produce as many seeds. Thereby they enlarge the reproductive output of the genet. Size-dependent survival of rosettes shows the same tendency as age-dependent survival. The small rosettes carry the risks in the wet site but in the dry site these risks are equally shared between small and big plants. Herbivore damage is concentrated in the smaller categories in the wet meadow and in the larger categogies in the dune grassland. This is the result of the differences in the most important herbivores in both sites: slugs in the marsh and rabbits and large grazers in the dune grassland. The prostrate ears are relatively well protected in the dunes but there is surprisingly high predation on the tall inflorescences in the hay meadow, which are eaten mainly by birds such as wood pigeons, ducks and pheasants.

3.3. Reproductive effort

The differences between both ecotypes are most pronounced in the way offspring is produced. Not only are there differences in the time to first flowering and the number of times a plant can be expected to flower, but also in the percentage of adults flowering and the amount and the partitioning of the energy invested in the offspring. The morphological aspects of seed production are summarized in *table 3*. At the dry site rosettes produce few, small and highly variable seeds per ear, but on many ears, also in side rosettes, and over a prolonged period of time. In all, about 147 seeds are produced as an average per genet. In the wet meadow this is about 103 seeds, produced by a few big spikes in late spring. Taking the lifespan of individuals into account, however, more seeds per adult are produced in the wet site. This can compensate for the greater risks for seeds and seedlings in the marsh. Such risks are much smaller at the dry site, where adults share the risks more or less equally with the young plants. These findings support the theoretical conditions formulated by CHARNOV & SCHAFFER (1973) for polycarpy, which state that the most pronounced polycarpy should be found when juvenile mortality is high compared with the risk of dying for adults.

There are indications that more costs are involved in producing offspring at the dry site than at the wet site. Not only are the seeds smaller and more variable but there is also a significant negative correlation between the mean seed weight in an ear and the number of seeds that can be filled per length of ear (*table 4*). The relationship between the number of offspring and the costs to produce them has also been used to predict the number of times an organism should reproduce (GADGIL & BOSSERT 1970). It states that polycarpy can be expected when the costs to produce offspring are low and when a higher reproductive effort does not result in a proportionally greater number of offspring. Monocarpy on the other hand can be expected when the costs to produce offspring are high, but greater reproductive effort results in a still greater number of offspring. This relationship can be approximated in this case by using the number of seeds as an equivalent for number of offspring and seed weight per cm^2 of leaf area as reproductive effort (*fig. 5*). The pros and cons of measuring
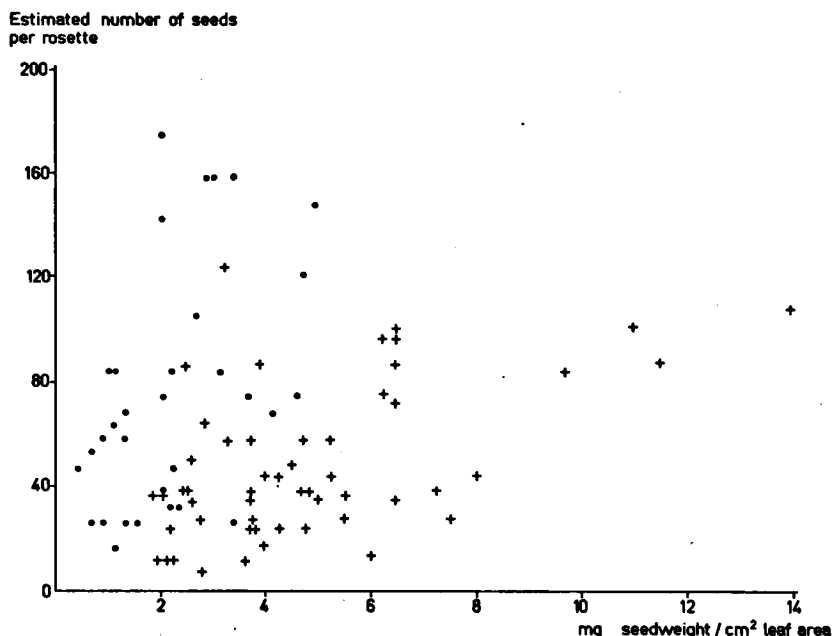
Estimated number of seeds
per rosette

Figure 5. Estimated number of seeds per rosette of *Plantago lanceolata* from a dry dune grassland (+) or from a wet meadow (●) as a function of reproductive effort, expressed as mg seed weight produced per cm² of leaf area.

Table 5. The relation between estimated biomass (EB) and reproductive effort (RE) measured in 43 rosettes of *Plantago lanceolata* from a wet meadow that flowered in the first season, and future reproductive success. Rosettes are categorized according their subsequent fate: ● flowering; ○ non-flowering and + dead.

		●+ 5	●○+ 4	●○○ 14	●○● 6	●●○ 5	●●● 9
1st year	EB	78 ± 72	76 ± 66	161 ± 151	203 ± 58	137 ± 67	286 ± 260
	RE	3.7 ± 3.0	2.9 ± 2.3	2.9 ± 2.0	2.1 ± 1.3	2.6 ± 2.2	2.1 ± 1.2
2nd year	EB	+	246 ± 118	173 ± 88	345 ± 198	274 ± 148	394 ± 482
	RE	+	−	−	−	1.0 ± 0.8	1.9 ± 1.2
3rd year	EB	+	+	148 ± 69	113 ± 50	146 ± 81	156 ± 102
	RE	+	+	−	6.7 ± 2.8	−	3.3 ± 1.7

reproductive effort as a ratio between plant parts are worked out by several authors (THOMPSON & STEWART 1981; WATSON & CASPER 1984). Nevertheless, this measure of reproductive effort is adopted here on the basis of the findings of PRIMACK (1979), who found a satisfactory relationship between this way

of expressing reproductive effort and polycarpy in the genus *Plantago*. The relationship between number of seeds and reproductive effort shows that in the wet meadow more seeds are produced at considerable lower costs than in the dry dune grassland. This is in agreement with theoretical predictions and with the findings of PRIMACK (1979). Moreover, these costs are significantly correlated to the number of seeds produced in the dry dunes, and this is a necessary condition for selection in the direction of monocarpy. At the wet site this correlation is not significant (*table 4*). This is not to say that there is no price to pay. This becomes evident when the biomass allocated to seed production is compared with the biomass allocated to growth over the flowering period. There is a clear negative correlation between RGR and reproductive effort in both habitats (*table 4*).

The other relationship used by GADGIL & BOSSERT (1970) to predict whether an organism should be monocarpic or polycarpic, is the relationship between reproductive effort and the residual reproductive value. It states that high reproductive effort should be associated with a reduced reproductive success in the future. This can be checked in the wet meadow, where the adults remained alive during the three years of field work. Out of 43 flowering rosettes in the first season, 5 died, 24 skipped flowering and 14 flowered again in the next season. The reproductive effort was highest in the group that died and lowest in the group that flowered again (*table 5*). Out of the 14 rosettes that flowered in the second season 9 did flower for the third time in the third season and this is significantly better than expected from the proportion of individuals that flowered twice ($\chi^2 = 5.24$; DF $= 1$; p < 0.05). This again is in agreement with the predictions and field evidence for instance for ecotypes of *Poa annua* (LAW 1979). However, without information on the genetics of reproductive effort, it is dangerous to interpret the field experience with these two ecotypes of *Plantago lanceolata* in an evolutionary context as selection for reduced polycarpy.

4. CONCLUSIONS

The complete demographic profiles for the two populations of *Plantago lanceolata* presented in this paper show clear contrasts that can be used for testing the theoretical predictions from life history theories, presented in the introduction.

The population in the dry dune grassland is found in an unstable environment under strong abiotic control. The soil is poor in nutrients and there is frequently a shortage of water, which sometimes takes the form of catastrophic droughts. The population is short-lived with juveniles and adults carrying about equal risks of dying. There is only a short juvenile period and plants flower in the next season. Seed production itself shows a clear size dependence and is found in small as well as in big rosettes. Seeds are produced from many short inflorescences at great costs. Within one spike a limited amount of resources is distributed over the embryo's present, resulting in small seeds. The seeds have a short period of innate dormancy and to some extent require light and relatively high

temperatures for germination. These germination requirements are consistent with the presence of a substantial seedbank as well as with the observation that the main germination takes place in spring. All this combines into a picture of a short-lived ruderal with a tendency towards monocarpic production of many small seeds which form a seedbank to tide the population over periods of unpredictable droughts.

The population from the wet meadow is found in a more stable environment and probably under strong biotic control as a result of vigorous competition by its neighbours, mainly for light. Shortage of light penetrating through the canopy to the soil surface is the main reason why so many seedlings and juveniles die in this habitat, whereas the adults, once they have penetrated into the canopy, live for long periods. Plants remain vegetative for at least three seasons. Only a relatively low percentage of all adults do flower. When flowering, rosettes produce one or two tall inflorescences at relatively low costs. The costs are paid in terms of reduced growth for the rosette over the period of seed production, but there is no clear relation between reproductive effort and number of seeds produced. The reproductive effort affects to some extent the future reproductive succes. The seeds have only very reduced innate dormancy. There is no requirement for light and germination proceeds at low temperatures resulting in direct germination in autumn and the presence of only a transient seedbank. This combines into a picture of a competitive, longlived, polycarpic perennial adapted to live in stable environments.

In summary, the hypotheses derived from the r- and K- selection theory are supported best by evidence from the field. In 'unstable' environments there is a greater adult mortality, a tendency towards monocarpy, many small seeds that are produced at relatively high costs and a short adult longevity. Time to first reproduction is shorter, but only when the period between germination and first flowering is considered. When the time spent in the seedbank is taken into account, time to first reproduction could actually be longer in the 'unstable' environment as required by the theory of bet-hedging.

5. ACKNOWLEDGEMENTS

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