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SELECTION
FOR
DIFFERENT
LIFE HISTORIES
IN
PLANTAGO
LANCEOLATA



Jan van Groenendael

SELECTION FOR DIFFERENT LIFE HISTORIES

IN *PLANTAGO LANCEOLATA* L.

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SELECTION FOR DIFFERENT LIFE HISTORIES

IN *PLANTAGO LANCEOLATA* L.

proefschrift

TER VERKRIJGING VAN DE GRAAD VAN DOCTOR
IN DE WISKUNDE EN NATUURWETENSCHAPPEN
AAN DE KATHOLIEKE UNIVERSITEIT TE NIJMEGEN,
OP GEZAG VAN DE RECTOR MAGNIFICUS PROF.DR. J.H.G.I. GIESBERS
VOLGENS BESLUIT VAN HET COLLEGE VAN DEKANEN
IN HET OPENBAAR TE VERDEDIGEN
OP DONDERDAG 23 MEI 1985
DES NAMIDDAGS TE 2.00 UUR PRECIES

door

jan marie van groenendael

geboren te Maastricht

1985

" Het dagelijks werk van de wetenschap bestaat voor het grootste deel uit het doen van waarnemingen en experimenten die erop zijn gericht om uit te zoeken of de denkbeeldige wereld van onze hypothesen overeenkomt met de werkelijkheid. En zo ligt aan iedere vooruitgang in onze kennis van de natuur een daad van verbeeldingskracht, een speculatief avontuur, ten grondslag. Het was geen wetenschapper of filosoof die als eerste deze geestesinspanning wist thuis te brengen en er de juiste term voor vond maar een dichter.... "

" (Poëzie) is middelpunt en omtrek van kennis tevens; ze is dat wat alle wetenschap in zich vat, en dat waaraan alle wetenschap moet beproefd worden. Ze is tegelijk de wortel en de bloesem van alle stelsels van denkingen, dat waaraan alle ontspringen en dat alle bekoorlijk maakt.... "

P.B. Medawar (1984). The Limits of Science. (vertaling J. Klerkx)

P.B. Shelley (1821). A Defence of Poetry. (vertaling A. Verweij)

CONTENTS

Voorwoord	6
1 General introduction	9
2 Teratology and metameric plant construction	19
3 Life history characteristics of two ecotypes of <i>Plantago lanceolata</i> L.	33
4 The contrasting dynamics of two populations of <i>Plantago lanceolata</i> L., classified by age and size	57
5 The significance of differences in life histories between populations of <i>Plantago lanceolata</i> L. from contrasting habitats using reciprocal transplant experiments: The importance of plasticity	85
6 Differences in life histories between two ecotypes of <i>Plantago lanceolata</i> L.: The possible importance of architecture	113
Summary	135
Samenvatting	139
Curriculum vitae	143

VOORWOORD

Dat dit proefschrift door een persoon wordt verdedigd, houdt niet in dat het ook de prestatie van een persoon is. De verantwoordelijkheid ligt bij mij, maar de verdiensten bij vele anderen. Het proefschrift is het resultaat van een lang maatschappelijk en wetenschappelijk proces, dat zo intens is dat het tot een onomkeerbaar engagement leidt. Het is daarom goed vooraf verantwoording af te leggen van de voornaamste determinanten in dit proces.

Allereerst zijn dat mijn ouders, die, tegen de feiten in, zicht hebben gehouden op de potenties in mij en me in staat hebben gesteld "tweede kans onderwijs" te volgen, lang voordat die term was uitgevonden. Ten tweede is dat Madeleine. De kiem van dit proefschrift is gelegen in haar voortvarendheid in het exploreren van nieuwe perspectieven. De confrontaties die hieruit voortkwamen, hebben een belangrijke verbreding opgeleverd van menselijke en wetenschappelijke inzichten. Wat wezenlijk is aan wetenschap, de ethiek maar vooral de esthetiek, is mij bijgebracht door Victor Westhoff. Het plezier in de uitdaging om problemen tot de kern te analyseren, komt voort uit het enthousiaste voorbeeld van John Harper. Zij beiden zijn de ware "bevorderaars" van deze studie.

Bij het bewerken van dit proefschrift is gebleken dat een goed platform voor wetenschappelijke discussie een onontbeerlijke stimulans is. De verantwoordelijkheid hiervoor lag bij Peter van der Aart, die in die zin de grenzen en de richting van het onderzoek heeft bepaald. Voor de dagelijkse begeleiding van het onderzoek kon ik te allen tijde een beroep doen op Kees Blom. Zijn goede raad zit verweven in de verschillende experimenten die zijn uitgevoerd, samen met de praktische adviezen van Joop van Heeswijk. Meer in het algemeen geldt dat de collegiale sfeer en de onderlinge vriendschap op "Weevers' Duin" een belangrijke rol hebben gespeeld bij het plezier in het werk, waarvan dit proefschrift een neerslag is.

Belangrijke verbeteringen van de inzichten die uit dit onderzoek voortvloeien zijn te danken aan de diepgaande discussies met Jos van Damme en Alt Smit. Vooral het nuchtere commentaar van Jos heeft bijtijds een eind gemaakt aan al te wilde speculaties. Verschillende studenten en stagiaires hebben meegewerkt in het onderzoek. Veel van hun werk is niet meer afzonderlijk aan te wijzen in de tekst maar hun bijdragen aan het denkproces kon ikzelf nog zeer goed herkennen bij het schrijven. Zij zijn in alfabetische volgorde: Bertie Joan van Heuven,

Eugène van Hove, Katrien Jansen, Trudy Piet, Philip Raaymakers, Pieter Reijbroek, Jeannet Vermuë en Cora van de Water.

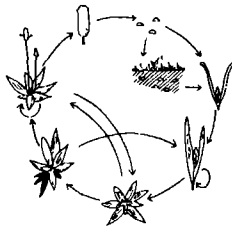
Bij het statistisch en rekenkundig verwerken van de grote hoeveelheid gegevens is de hulp van Peter van Ewijk en Pieter Slim onontbeerlijk gebleken. Tijdens het verwerken van de gegevens en tijdens het schrijven hebben Siny ter Borg en Aad van Ast stilzweigend en als vanzelfsprekend de gaten opgevuld die ontstonden door mijn preoccupatie met het proefschrift, inclusief een periode van drie maanden, die ik elders met toestemming van Piet Zonderwijk heb doorgebracht. Voor deze vriendendienst ben ik hen zeer dankbaar. Gedurende die drie maanden is mij door Jan Woldendorp gastvrijheid verleend op het Instituut voor Oecologisch Onderzoek te Heteren.

In diverse stadia van bewerking is door een aantal personen de tekst van kritisch commentaar voorzien. Dit heeft in een aantal gevallen tot aanzienlijke verbeteringen geleid en soms fouten voorkomen. Daarvoor bedank ik Kees Blom, Siny ter Borg, Jos van Damme, Wouter Joenje, Hans de Kroon, Richard Law, Bert Lotz, Jaap Mook, Rob Soekarjo, Peter van Tienderen, Jan van der Toorn en Jim White. Degenen, die het manuscript hebben gezien, weten met hoeveel inzet en nauwkeurigheid Ali Ormel orde in de tekst heeft aangebracht, waarbij de figuren zijn gemaakt door Herman Klees. Jan Klerkx heeft bij een aantal hoofdstukken suggesties gedaan om de engelse tekst te verbeteren.

Dit proefschrift is begonnen in een tijd van toereikende financiering van onderzoek. Vele jonge onderzoekers moeten zich nu vaak grote inspanningen getroosten tegen geringe vergoeding en met nog geringer perspectief. Van hun inzet hangt voor een belangrijk deel de toekomst af van dit vak. Aan hen wordt daarom dit proefschrift opgedragen.

"Verklaring" noemen wij het maar "beschrijving" is het, waardoor wij ons gunstig onderscheiden van oudere trappen van inzicht en wetenschap. Wij beschrijven beter - we verklaren net zo min als allen die voor ons kwamen.

F. Nietzsche



Het onderzoek waarop dit proefschrift is gebaseerd, is uitgevoerd op het Instituut voor Oecologisch Onderzoek, Afdeling Duinonderzoek "Weevers' Duin" te Oostvoorne. Het onderzoek werd gefinancierd door BION-ZWO in het kader van het zwaartepunt-project "Vergelijkend onderzoek naar demografische, fysiologische en genetische eigenschappen van plantesoorten in relatie tot hun standplaats in graslanden".

Grassland Species Research Group Publication No. 100.

chapter 1

GENERAL INTRODUCTION

The basic phenomenon that is at the heart of this thesis is the fact that, although species may differ in many ways, they can yet show a remarkable likeness in the ways in which they are adapted to their environment. There seem to be many more species than there are major ecological factors to which they must adapt. This basic observation is already very old and can be traced back at least to Von Humboldt (1806, see Werger, 1980). This phenomenon offers the possibility of generalization and therefore an opportunity for theory building. Many systems and their theoretical foundations have been presented, each system stressing its own ordering principle. The first one to use traits related to the life history of species as a criterium, was that of Warming (1895; 1909), whose system of life forms was based on the longevity of species. Another such criterium was that of Raunkiaer (1904) based on the position of dormant buds in relation to survival in the adverse season. Common to all these systems is the notion of adaptation to a specific environmental factor. Lately the term strategy or tactic has come into use to describe more complex adaptations which occur in species in response to more complex environmental factors (Grime, 1979; Stearns, 1976), ignoring the useful distinction between these two concepts made by Harper (1967).

A rather ornate branch on the tree of theories that seek to explain the various patterns of convergence in the ecology of species, is the theory that tries to find an explanation for the similarities in pattern of life histories between species. In a widely cited review of this life history theory, Stearns (1976) describes this pattern as a life history tactic. A tactic in his definition is 'a set of co-adapted traits designed, by natural selection, to solve particular ecological problems. A complex adaptation'. Apart from the teleological aspects, such a tactic in the context of the life history theory refers to a combination of co-adapted life history traits such as age- and size-dependent fecundity and mortality, number and individual size of offspring, time to first reproduction and frequency of reproduction, longevity and senescence. The basic justification for the existence of pattern in life history traits is rooted in the allocation principle which states that organisms have a limited amount of resources which they can allocate to reproduction, survival and competition, resulting in particular trade-offs (Skutch, 1949, Cody, 1966). There are many studies which demonstrate this principle, and a large body of theoretical

models has been developed, based on the optimization of allocation. Recently the notion of trade-offs has been called into question as far as plants are concerned, because of the relative autonomy of various plant parts, at least with respect to allocation of carbon (Watson, 1984; Watson & Casper, 1984). If such autonomy exists, then the way various plant parts develop and are allocated to various functions becomes very important. In that case the optimization of allocation of resources should be complemented by the optimization of design (Smith, 1984).

The kind of environmental characteristics which determine a life history tactic are usually defined loosely in terms of density dependence in the regulation of the size of a population or in terms like predictability or "grain" of the environment. It is this ambiguity which hampers the development of a unifying theory (Boyce, 1984) so that a broad complex of theories of lower order exists, which lead to statements with regard to one life history trait or a combination of various life history traits (Stearns, 1976; 1977). The question remains what makes life history theory so exciting that such a large, mathematically often elaborate body of theory has developed, making predictions on life history traits faster than tests of the hypotheses can be produced? The answer lies in the fact that in life history tactics there is a point of common interest between population ecologists and population geneticists (Barbault, 1984; Loeschcke & Wöhrmann, 1984). This interest is based on the fact that life history traits define the fitness of an individual. It is through differential survival and reproduction that some organisms show a larger increase in abundance than others, causing changes in the frequencies of the genes they carry with them. Or, quoting Stearns (1984) 'Life history traits are the phenotypic components of fitness'. Any evolved and co-adapted pattern in life history traits could therefore improve our understanding of the process of evolution.

In this thesis the evolution of life histories is studied following a scheme which has been successfully applied in genecology. In this field of research, where ecology and genetics have long since met one another (Heslop-Harrison, 1964; Langlet, 1971), the following propositions are made, (from Heslop-Harrison, 1964):

1. Wide-ranging species show spatial variation in morphological, physiological and in this case life history traits.
2. Much of this variability can be correlated to habitat differences.

For life history traits this point is reviewed in Stearns (1976, 1977).

3. Much of this variability has a genetical basis.
4. That part of the variability which is correlated with the habitat and has a genetical basis, is the result of natural selection.

The first point of this scheme restricts the study of evolution of life history tactics to intraspecific comparisons. In contrast to his earlier opinion (Stearns, 1976), Stearns (1980) argues that complex co-adaptations in life history traits will probably be rigid like the trait complexes which define the morphology of species, and are therefore best studied at higher taxonomical levels, using broad surveys, instead of at the level of intraspecific variation. However, there is no a priori reason why complex adaptations should be rigid. In the case of morphological traits which define a species, there is a clear advantage in rigidity, because reproduction may depend on it. On the other hand, as argued by Harper (1982), there seems to be no reason for rigidity in traits that are geared toward maintaining individuals in more or less variable environmental conditions. Therefore, intraspecific variation in life history traits might still offer the best opportunity for studying the evolution of life histories (Egges, 1982; Barbault, 1984).

The third point of the scheme has to be amended to include genetic covariation between life history traits, as required by the definition. Relatively few studies demonstrating this genetic covariation have been published so far. Most of these studies were carried out by breeders, who tried to maximize certain aspects in plants or animals related to reproductive output and found their efforts restricted by correlation with other traits (Egges, 1982; van Dijk, 1985). Some evidence for genetic covariation in traits regulating seed yield in *Plantago lanceolata* is presented by Primack & Antonovics (1981).

The last point of the scheme is a conclusion based on reasoning after the fact and on analogy. Proof by analogy is not rated high in scientific theory, but it is still open to debate whether evolutionary hypotheses can be proven in a strict scientific sense (van der Steen, 1983a; Thompson, 1983). Somewhere in between strict proof and pure analogy is the hypothesis that the observed differences in life history traits must result in differences in fitness between individuals, thus making the evolutionary process more plausible. This hypothesis will be approached in two ways, in a direct test and in an indirect way, using model simulations.

A direct test on differences in fitness can be performed by reciprocal transplant experiments as advocated by Antonovics (1976). Although transplant experiments are not new (Bonnier, 1890; for a historical review see Briggs &

Walters, 1984) the reciprocity provides many additional advantages. It allows testing not only of the genetical aspects (Antonovics & Primack, 1982) but also of the plastic response, especially if cloned material is used in the transplanting. This important aspect of a plant's capacity to maintain itself in a variable environment (Bradshaw, 1965) has been considered a nuisance in evolutionary ecology, although recently plasticity has received renewed attention (Caswell, 1983; Stearns, 1984; Kuiper, 1984).

The indirect test uses a matrix projection model (Lewis, 1942; Leslie, 1945), with which the dynamics of a population of a species can be simulated. The model's parameters are life history traits such as fecundity and survival, and these are estimated from field observations. The most important simulation result is an estimate of the population growth rate. The usefulness of this type of model in an evolutionary context has increased considerably since Caswell (1978) developed a general sensitivity analysis for these models. The reason is that the sensitivity analysis shows which parameter has the greatest impact on the population growth rate and therefore on the fitness of the individuals in the population, using Fisher's theorem (Fisher, 1958). Sensitivity analysis therefore predicts where to expect the highest selection pressure in the life history of an organism and this in turn can be translated into quantitative genetic hypotheses about the levels of additive genetic variance to be expected. (For an early example of the use of sensitivity analysis in an evolutionary context, though based on a different type of model, see Lewontin, 1965). It should be kept in mind, however, that this is an indirect test and that it relies heavily on the population growth rate being an appropriate measure of fitness. This certainly is open to debate (Cooper, 1984).

The points raised in this introduction are explored using *Plantago lanceolata*. *Plantago lanceolata* has been chosen as the species to use in this study for several reasons. This species occurs widely in a variety of mainly grassland habitats. It is reported to form ecotypes quite readily (Böcher, 1943; Primack, 1976), and the species of *Plantago*, that are found naturally in The Netherlands, had been selected for a large scale, interdisciplinary investigation of their demographical, physiological and genetical characteristics in relation to their occurrence in grassland habitats (Van der Aart, 1979).

The subsequent chapters of this thesis deal with the following aspects. Chapter 2 explores the way in which a rosette of *Plantago lanceolata* develops, based on how different meristems are assigned to different functions. This may

affect the allocation pattern, which is the fundament of any life history tactic. In chapter 3, the different life histories of two ecotypes of *Plantago lanceolata* are described in relation to habitat characteristics. Special attention is given to reproductive effort, this being the most important aspect of the allocation pattern. In chapter 4, the demographic data collected in the field are transformed into matrix model parameters. After testing, a sensitivity analysis is applied to these models and several new hypotheses are formulated. Chapter 5 discusses the differences in fitness that are the result of differences in life history traits in a series of three reciprocal transplant experiments, each experiment testing a different phase of the life history. One of the tests was done using cloned material and can therefore be used to discuss the effects of plasticity. The last chapter provides a kind of synthesis in which the model's predictions will be compared with the results of the transplant experiments.

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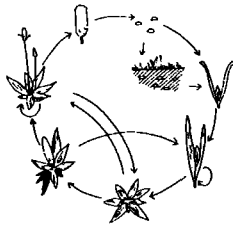
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Part of this chapter is published under the same title in *The New Phytologist*, 99, 171-178.

Grassland Species Research Group Publication No. 80.

TERATOLOGY AND METAMERIC PLANT CONSTRUCTION

SUMMARY

The growth of *Plantago lanceolata* L. has been described using metamers as construction units. The growth of each unit has been broken down into a sequence of four simple building instructions, two of which incorporate two or three alternatives. The resulting conceptual model has been tested against a variety of teratologies known to exist in *Plantago lanceolata*. All of these malformations could be explained in terms of either wrong steps, or wrong sequences, or both. There seems to be a certain hierarchy of control such that more malformations tend to occur at tertiary meristems than at primary meristems. For at least some of the teratologies, the nature of the control seems genetic.

In plant ecology growth phenomena have been studied from different points of view. A first approach emphasizes growth as a process of capturing resources, studying its efficiency, allocation and evolutionary basis (e.g. De Wit, 1960; Brouwer & De Wit, 1968; Grime & Hunt, 1975; Hunt, 1978; Abul-Fatih, Bazzaz & Hunt, 1979). This approach has its roots mainly in agronomy.

Another line of thinking, one that will be adopted here, considers growth as the rhythmic and iterative development of a plant, studying the functional and adaptive characteristics of shape, either as a whole (e.g. Hallé & Oldeman, 1970; Tomlinson, 1982) or as a result of the dynamics of plant parts (e.g. Harper & White, 1974; Harper & Bell, 1979; Caloin, Malonga & Tricart, 1983). It has its roots in plant morphology (White, 1979; Cusset, 1982).

A common objective for morphologists and plant ecologists is the understanding of the rules of development, the controls involved (genetic or environmental) and their evolutionary basis. The objective has been pursued at different levels of organization. In this respect the modelling of plant shape has been used heuristically to find rules at the cellular level (Lindenmayer, 1975) and at the metameric level (Bell, 1976). One type of model which has been used to construct multicellular arrays can with some slight modifications be used to construct models of whole plants (Frijters & Lindenmayer, 1974). A second approach models the shape of a plant directly using a basic unit of plant construction or metamer (White, 1979). This type of model has been used to simulate the development of ramets as well (Bell, 1979, 1984).

It is the aim of this paper not only to show that a model using the metamer approach is capable of summarizing gross developmental processes in another genus (*Plantago*), but also that without difficulty the same model can be extended and used to construct and predict a wide range of teratological malformations that have been found in Plantains, a genus long known to be notorious in this respect (e.g. Penzig, 1894). It is argued that the study of teratological malformations, using metameric plant construction, can suggest aspects of plant development where regulatory processes can easiest be disturbed. This could help the understanding of plant morphogenesis (Sachs, 1982).

MATERIAL

During the summer of 1980 about 40 teratological individuals of *Plantago lanceolata* L. were collected in an abandoned meadow near Eben-Emael in Eastern Belgium. The collection included examples of a variety of abnormalities that occurred with unusually high frequency of about 1% of the flowering individuals in that meadow. The material was photographed, dried and when necessary studied under a binocular microscope. Teratological material of other plantains (*Plantago major* L., *Plantago coronopus* L.) was made available by J. van Damme (State University of Groningen). Also, information from the literature has been used (Penzig, 1894; Blaringham, 1923, Anonymous, 1926; Troll, 1943; Garjeanne, 1951). Seeds were collected from some of the teratological individuals, sown in the greenhouse in the spring of 1983 and grown to maturity to find if there were any teratologies in the progeny (see also Blaringham, 1923).

THE MODEL

The model that will be used in this paper is conceptual rather than mathematical and uses as its basic unit of construction, a metamer: i.e. an internode, a node and the leaf attached to it with its axillary meristem. The construction of the metamer has been broken down into four simple 'building instructions to a meristem': 1, form an internode and suppress its elongation or 1a, form an internode, that will elongate; 2, form a node and a normal leaf at position x (degrees) or 2a, form a scale-like leaf (bract) or 2b, form floral initials; 3, form an axillary meristem at position x (degrees); 4, rotate n degrees.

By iterating 1 to 4 a description of a normal vegetative rosette of a plantain is given. This includes a population of axillary meristems (or second order meristems). These axillary meristems may remain dormant or they may be stimulated into growth following one or other of two possible sequences: an iteration of 1, 2, 3, 4 will describe the formation of side rosettes, while the instruction 1a, 2a, 3 and 4 followed by an iteration of 1, 2a, 3 and 4 will describe the formation of a flowering stem and spike. The third order meristems in the side rosettes are equivalent to the second order meristems of the main rosette and by following 1, 2, 3, 4 cause a rapid proliferation of potential branching points. To model the formation of the flowers the third order meristems follow the sequence 1, 2b which in this model is final. Floral or-

gans are thought to be modified leaves, and in a more detailed model the formation of sepals, petals, stamens, pistil and ovary might be achieved by variants of the main sequence of 'building instructions' outlined above. For our present goal, these details can conveniently be summarized in one step, 2b. The description which this model provides of the development of a normal rosette of *Plantago*, with several flowering stems and spikes, is summed up in Fig. 1, though without using the stopping rules that will be discussed later on. The description resembles in form the model of Rauh, as described by Jeannoda-Robinson (1977). It applies to all species with a basic architecture similar to that of *Plantago*.

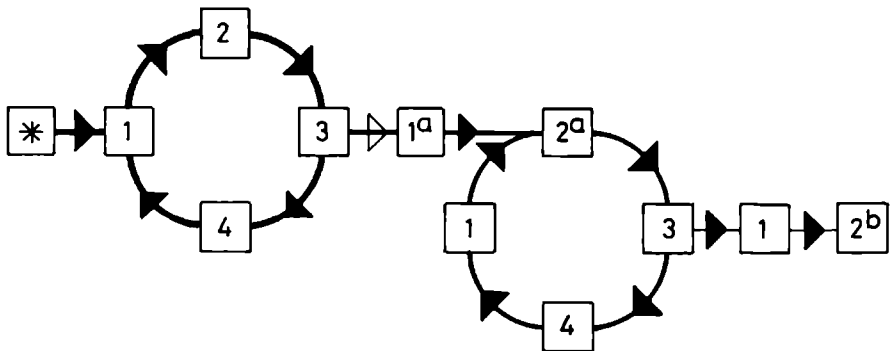


Figure 1. Construction pattern for a single, flowering rosette of *Plantago*, using metamers. Numbers refer to construction steps (see text)
 Key * Moment of germination, — Developmental path in first order meristem, — Developmental path in second order meristem, — Developmental path in third order meristem, ► compulsory step, ▷ optional step.

TFST OF THE MODEL

The model has been tested against various malformations which have been observed in *Plantago lanceolata* L (Fig. 2).

The first set of malformations (A to H) can be attributed to 'wrong steps', A to C by an error at step 1, D to F by an error at step 2 and G to H by an error at step 4. None of these errors involves step 3. However, whether step 3 is executed or not is sometimes difficult to notice. Only when an axillary

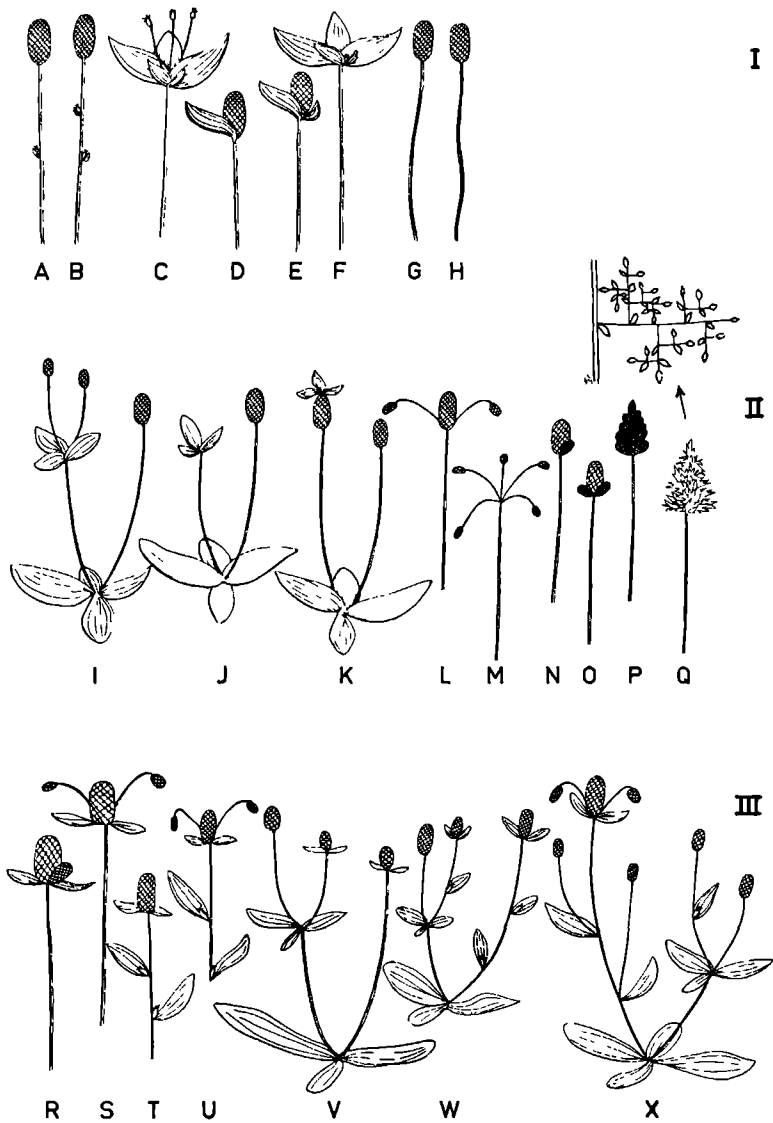


Figure 2. Teratologies in *Plantago lanceolata*. I, wrong steps; II, wrong orders; III, combination of I and II (for further explanation see text).

meristem must develop into something, as for instance by the obligatory formation of a flower by a third order meristem, can abnormal development be identified. Malformations A to C involve an error in step 1. Step 1 is expected; if step 1a is executed instead, then A results; if step 1a is executed repeatedly B results; if step 1a occurs at a third order rather than at a second order meristem C results, but always in combination with a fault in step 2. Errors in 1 at a first order meristem have not been observed. Step 2 can be executed instead of step 2a in second order meristems, forming leaf like bracts, once (D), a few times (E) or all the time (F). Note the flowers in the axils with F, which makes it distinct from J (see below). Leafy spikes are also known for *Plantago major*, where it is a hereditary feature known as the (fertile) var. *rosarius*. Whatever mistakes can occur in the third order meristem are hidden in the general step 2b, but errors such as wrong numbers of sepals, leaf-like stamens (one of the forms of male sterility, see Van Damme & Van Delden, 1982), are known to be of common occurrence. Whether mistakes are common in step 4 is difficult to tell without measuring the actual parastichies of the rosette or the spike, except for one case, the rather common, simple or multiple, distortion of the flowering stem (G, H). It appears that 'wrong steps' are more common in second and third order meristems than in the main meristem.

The second set of malformations (I to Q) are ascribed to 'wrong orders', that is, sequences otherwise correct are executed at the wrong moment in the model. For instance, when a rosette is found with a central flowering spike produced by the first order meristem, this is described by the model in terms of a first order meristem acting like a second order meristem. The situation where the main meristem forms a flowering spike has only been observed in *Plantago coronopus* (J. van Damme, personal communication). Second order meristems may execute first order programs to result in side rosettes which are found in nature. When the first order program is executed after step 1a, this should result according to the model in stalked rosettes, like the ones found and drawn as I and J. If the second order meristem reverts to a first order sequence, when the flowering spike is already nearly completed, then the model describes a situation like the one under K. This malformation has sometimes wrongly been described as vivipary. The absence of flowers in the leaf axils indicates that only a wrong step is insufficient to model this teratology; a complete first order program is necessary (compare F and J). Teratologies like L and M can be expressed in terms of the model as a third order meristem exe-

More complex combinations of wrong steps and wrong sequences in the collected material are listed under III in Fig. 2. The combinations are R:E+N; S:E+L; T:A+E; U:A+E+L; V:E+I; W:A+E+I and X:A+E+I+L.

From these examples, it is clear that the simple growth model presented in Fig. 1 can describe the more complex teratologies known for *Plantago lanceolata*. For convenience all the possibilities are summarized in Fig. 3.

The phenotype of progeny of aberrant parents

Seeds from the collected material of type O, P, U and X were sown in the greenhouse, grown to maturity and checked for teratologies. The results are presented in Table 1. Not all original aberrations presented in Fig. 2 could be tested this way, because not all individuals contained ripe seeds and some (Q) were sterile. The results show that type O and P recur in progenies derived from O and P parents; while types U and X do not. A more comprehensive study was reported by Blaringhem (1923) who obtained 80% of teratological spikes of type L-Q, in progenies after three generations of backcrosses between male sterile seed plants and pollen from aberrant types.

Table 1. Tests on the progeny, grown from seeds from open-pollinated teratological parental plants (letters refer to Fig. 2).

Plant number	Phenotype	Number of seedlings raised	Number of teratomas	Phenotype
1	O	25	2	O
2	O+P	25	1	O
3	O+P	25	0	-
4	O+P	25	3	O+P
5	P	25	2	P
6	P	12	1	P
7	U	25	0	-
8	X	12	0	-

Ideally, the model that conveys most understanding of the processes that regulate growth and gross morphology of a plant individual should be a mechanistic one and ultimately be based on the phyllotaxis of plants as argued by Jean (1983) in a stimulating review. All of these processes are of interest to a plant ecologist, because vital functions of a plant depend on orderly, sequential development of tissues and organs and these developments in the end are under direct or indirect environmental control (Sattler, 1982; White, 1984). In an ecological context such detailed models are only seldom used because of the detail and the complex relationship with environmental determinants through the cell physiological level. It is therefore not surprising, that the model used most by ecologists is more empirical and takes a more practical approach towards the phenomenon of growth, considering the whole plant or large parts of it like root, shoot, generative parts etc. and measuring its reaction to environmental conditions in terms of dry weight or rates of change in dry weight or any other appropriate unit.

The model presented here, like other models based on metamers, is essentially mechanistic. It is capable of accounting for all observed teratomas in *Plantago* in terms of errors in a set of 4 repetitive construction steps. This way the usefulness of the model is confirmed. For future use the model could be improved by including the appropriate plastochron times and growth rates for plant parts (Hunt, 1978; Hunt & Bazzaz, 1980; Gounot, Yu & N'Kandza, 1982). By putting construction costs to the architecture, a set of stopping rules could be provided and the various options a plant has to use its potential of meristems (Maillette, 1982; Porter, 1983) could be tested more extensively.

However, if the metameric plant construction model is to be anything more than a tool to mimic reality under different sets of rules, it must be capable of working heuristically and hint at the very nature of these rules. As pointed out by Sachs (1982) different levels of control should exist which must act upon the processes of development and be conservative in early stages. How such a hierarchy of controls could work is demonstrated by the work of De Vries, Springer & Wessels (1982, 1983). In developing pea seedlings there was no difference in abundant and polysomal m-RNA content in different organs, like roots, shoot, epicotyl and cotyledons, suggesting an epigenetic control of morphogenesis in this phase. In adult tobacco plants up to 70% of at least the polysomal m-RNA's is organized in an organ-specific manner (Kamalay &

Goldberg, 1980). This suggests a shifting balance between epigenetic and direct genetic control in the process of morphogenesis, shielding the young plant with a relatively unexpressed genotype from direct selective action from its environment, providing a hierarchy of control.

Whatever the nature of the control, its hierarchy seems obvious. In the case of *Plantago lanceolata* for example, it seems that a first order meristem has no other option than to maintain and preserve the vegetative rosette. No teratologies are known in the main rosette of *Plantago lanceolata* and control here is tight and conservative. The second order meristem can produce either flowering stems and spikes or it can produce side rosettes which resemble the rosette, but second order meristems have not been observed to produce individual flowers. Teratologies are well known for this level (see Fig. 2, A to K) but seem to be environmentally determined, rather than by a change in the genotype (Table 1, U and X). The third order meristem can produce new spikes like the second order meristem, but unlike second order meristems it seems that these do not produce side rosettes. Although the formation of spikes within a spike is comparable with the formation of side rosettes in a main rosette, such forms (L to P) are considered teratological. These malformations and mistakes in flower construction are by far the more common teratologies, a fact also recognized by Blaringham (1923), and clearly have a genetical basis. Generally speaking there is a decreasing level of control as growth advances as postulated by Sachs (1982). But when things go wrong further away from the main meristem, they go wrong in a well organized, patterned manner even to the point of being heritable. Many malformations possible from the model have not been observed and those that have seem to arise in an opportunist fashion, several together, usually under peculiar circumstances, as a reaction on disturbances in the habitat. Blaringham mentions mowing too early or the application of organic manure in the middle of the growing season as causing teratologies. The material used for this paper came from an abandoned meadow, where a road was under construction. Spraying against mildew in the greenhouse with Dinocap, a dinitro compound that stimulates metabolism, appears to trigger teratologies like D and E (personal observation). The moth *Tortrix paleana* is reported to cause teratologies like N and O by depositing her eggs in the spikes of *Plantago lanceolata* (Darlington, 1968).

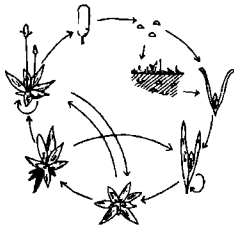
It is the capacity of the metameric plant construction model to simulate plant development and also to hint at the nature and level of control that regulates plant morphogenesis. In this respect teratological forms can be a valuable tool in understanding growth and how it is controlled.

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LIFE HISTORY CHARACTERISTICS OF
TWO ECOTYPES OF *PLANTAGO LANCEOLATA* L.

SUMMARY

The life history of two populations of *Plantago lanceolata* L. from contrasting habitats is described, using standard demographical techniques. One habitat is an open dune grassland on poor sandy substratum, grazed as a commonage for centuries. The vegetation occasionally suffers from drought. The other habitat is a closed hay meadow on organic substratum that is permanently waterlogged, 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 (subvar. *sphaerostachya* f. *minor*). The plantains in the wet site form few tall erect leaves and no side rosettes. Big seeds are produced from few long inflorescences on long stalks early in the season (subvar. *latifolia*). Seeds from the dry population show innate dormancy, that shifts the main germination period 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 life history theory.

Since Turesson's important work on intraspecific variation in plants in relation to habitat characteristics (e.g. Turesson, 1922a,b, 1925) and stimulated by the important evolutionary conclusions that can be drawn from such studies, 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 surprising that such a successful approach has also been advocated in a related but much younger field of evolutionary ecology: The evolution of life history tactics (Stearns, 1976; Etges, 1982; Barbault, 1984; but see Stearns, 1980, 1984). A tactic has been defined as a complex adaptation, as a set of co-adapted 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 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 theory, that has grown and is still growing without much empirical testing. According to Stearns (1976), a set of data to test the theory with should fulfil three criteria. The data should describe the life history in demographical terms with special attention given to reproductive effort, as this is a central concept in the theory. The tests on differences in life history tactics should preferably be performed using ecotypes of the same species and, lastly, the ecotypes must be subjected to differences in density-dependent regulation in the field, as this is another central concept in the theory.

Notwithstanding the fact that some of the best 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; Antonovics & Primack, 1982; Blom, 1983), these studies remain comparatively 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, due to the diffuse interactions between plants, it is difficult to define density dependence. It is therefore usually equated with competitive ability, regardless of the nature of the competitors, but, as was 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 provide empirical information with which at least some of the predictions of life history theory can be tested. For this purpose, two ecotypes of *Plantago lanceolata* from two contrasting habitats have been studied over a three year period, using demographic techniques. Further tests of the theory, based on these data, are presented elsewhere (Van Groenendael, 1985b,c).

MATERIAL AND METHODS

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 (Ross, 1973) and each flower contains two ovules. It produces relatively large, smooth, oblong seeds about 3 mm in size, 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°C to 30°C, with an optimum around 23°C and to be stimulated by fluctuating temperatures (Steinbauer & Grigsby, 1957; Blom, 1978; Grime et al., 1981). Silvertown (1980) reports inhibition of germination under leaf canopies, but this is not confirmed in experiments by Gorski et al. (1977) and by Pons (unpubl. data) using an artificial red/far-red gradient. Light sensitivity can be induced by burial (Wesson & Wareing, 1969) and germination is inhibited completely by far-red light in the seeds remaining after burial (Pons, unpubl. data). 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* forms two linear cotyledons, the shape of which seems to be genetically controlled (Antonovics & Primack, 1982; Slim & Van der Toorn, 1983). Growth rate can be quite high (Milton, 1943) but usually is found to be moderate (Grime, 1979). Although plants may flower within 6 weeks after sowing in the greenhouse or experimental garden, it usually takes individuals more than one season to flower in the field. Flowering is induced by long day conditions (Snyder, 1948). During growth a variable number of side rosettes are formed, which increases the number of axillary meristems from which inflorescences may originate (Soekarjo, 1980; Van Groenendael, 1985a), thereby increasing the reproductive output.

The genus *Plantago* is considered conservative in an evolutionary sense (Stebbins & Day, 1967), notwithstanding the worldwide distribution of some of its members as successful weeds. *Plantago lanceolata* itself grows in the Netherlands in a variety of mainly grassland habitats (Westhoff & Den Held, 1969; Haeck et al., 1981), tolerating a wide range of microclimatological (Stoutjesdijk, 1981) and edaphic (Troelstra et al., 1981) conditions. It is known to adapt to all these different 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).

Site description

Two habitats were selected which were sufficiently contrasting to allow straight-forward interpretation of differences in life cycle characteristics afterwards. The choice was confirmed by an ordination of all habitats of *Plantago lanceolata* (Haeck et al., 1982) based on the species assembly growing with *Plantago lanceolata* as the best overall indication of biotic and abiotic conditions (Westhoff & Van der Maarel, 1978). The first study site was located 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). This more or less guaranteed fairly constant selective pressures. The grassland consists of a complex of dry dunes and wet dune slacks, with *Plantago lanceolata* more

or less abundant in an intermediate situation. When comparing the vegetation of the dry site with the standard classification of all Dutch vegetation types (Westhoff & Den Held, 1969), this vegetation belongs to the class of the dry grasslands, and is intermediate between two alliances, Thero-Airion and Galio-Koelerion, as a result of the gradient on the slopes of the dunes (Blom, Husson & Westhoff, 1979). It is an open grass sward of low productivity on leached, formerly calcareous sandy substratum, which dries out easily. Consequently the vegetation suffers from periodic, but 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 show many leaves and ascending inflorescences with small roundish spikes, a form described in the literature as subvar. *sphaerostachya* Mert. et Koch f. *minor* (see Pilger, 1937). They form more or less clearly-defined patches, partly because of the many side rosettes formed in this population and partly because of limited seed dispersal. The plants flower late in the season, from July to September.

The second study site is a wet hayfield, which is mown once a year in the beginning of July. By that time all plants have set seed; plants flower in May and June. This meadow has been used for hay-making for a long period of time. 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 plantain have long erect leaves and erect inflorescences with elongated spikes on long scapes. This form is described in the literature as subvar. *latifolia* Wimm. et Grab. (see Pilger, 1937). Side rosettes are formed only rarely and the plants are distributed more or less randomly over a wide zone of the marsh.

Demography

In both sites a series of 3 quadrats was set out, each of 0.125 m^2 and marked with fixed cornerpoles over which a transparent drawing table could be fitted. The quadrats were placed close to each other in the centre of the same popu-

lation, where the density of plantains was greatest. Apart from winter time, all rosettes were recorded onto plastic sheets every 6 weeks. Each rosette was given a fixed number and its fate was followed over 3 seasons, 1979, 1980 and 1981. The following data were recorded: Number of leaves, length of longest leaf, 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 cotyledon 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 4 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 3 deeper layers, these were taken together in the analysis. After 3 months the soil was sieved to retrieve any remaining seeds. These were tested for viability using vital staining with 0.1% tetrazoliumchloride solution. In this way information was obtained on size and seasonality of the seedbank.

Given the contrasting information in the literature on the requirements for germination, germination tests were conducted during the winter of 1980. Three petri 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, till they were used. 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 as 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 in safe green light, 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 flower-

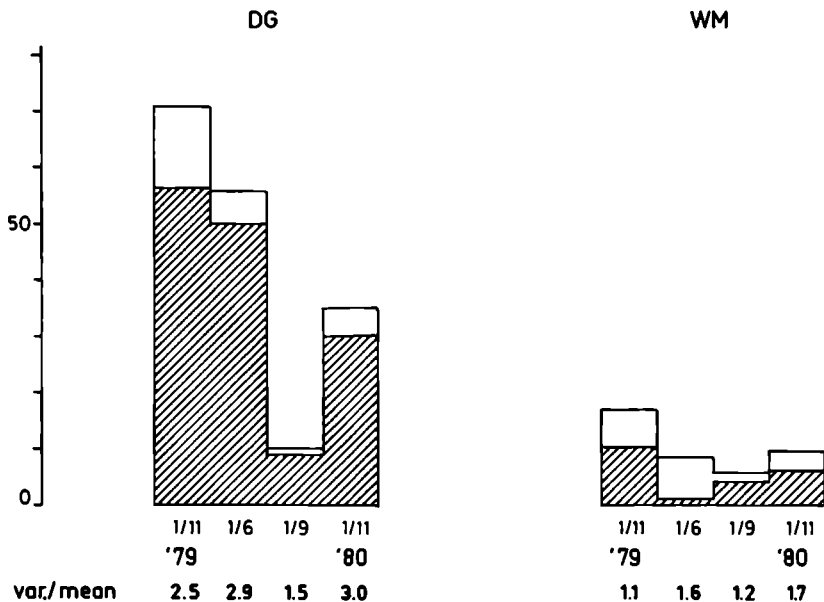


Figure 1. Number of seeds in the soil for *Plantago lanceolata* in a dry dune grassland (DG) and a wet meadow (WM) at 4 moments in the year, based on 50 soil samples each. The clustering of seeds in the samples is indicated by the variance over mean ratio. The number of seeds present in the top layer (0-1 cm) is indicated by shading. The remaining seeds were found between 1 and 10 cm.

ing season. About 30 adult rosettes were selected just outside the quadrats. The leaves and ears in these rosettes were marked with paint, using the technique described by Blom & Van Heeswijk (1984). The fate of 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.

RESULTS

Seedbank and germination

The life of an independent individual of *Plantago lanceolata* is taken to start as a seed in the soil or on the soil surface, which together form a seedbank.

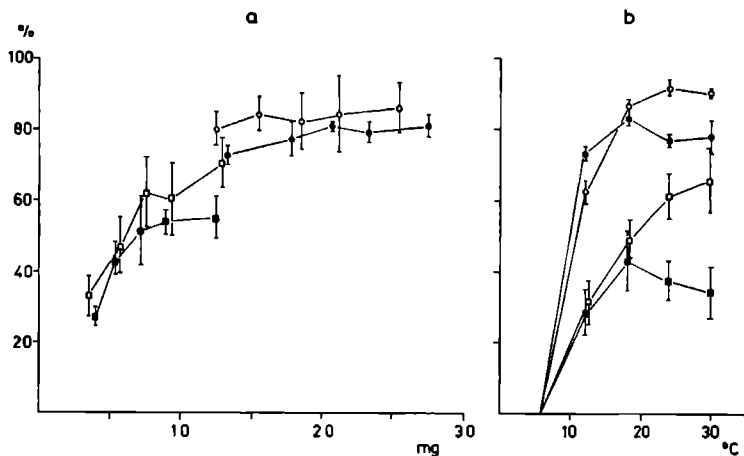


Figure 2. Percentage germination after six weeks, of vital, one year old seeds of two populations of *Plantago lanceolata* as a function of seed-weight, tested at 21°C (a) or as a function of temperature (b). The population from the dry dune grassland is represented by squares, the population from the wet meadow by circles. Open symbols refer to tests conducted in light, closed symbols to tests in dark. Bars indicate the standard error.

In the dry dunes this seedbank is larger, more concentrated in the top layer of the hard sandy soil and also more variable in time, but even at its smallest size it still contains twice the number of seeds that are found in the marshy soil of the meadow (Fig. 1). Here seeds are buried deeper in the soft substrate and show a less pronounced pattern in time and in space, as indicated by the variance over mean ratio (values closer to unity). In the dry dunes the spatial distribution is much 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 decreases with decreasing seed size in the dry dunes whereas there is no such effect in the bigger seeds from the wet meadow

(Fig. 2a). The response to temperature is also clearly different. Seeds from the meadow population germinate at lower temperatures than seeds from the dune population, but are also more clearly inhibited by high temperatures (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 dry and wet population, respectively). After twelve weeks this innate dormancy is relieved (percentage germination 74 ± 8 for dry and wet population, respectively).

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 must be possible at low temperatures and under low light intensities. There is little innate dormancy so that germination can take place in autumn or early in spring when the vegetation is relatively open. This is in agreement with the actual pattern in the field (see below). 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.

Population dynamics

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

More insight in the dynamics can be obtained by studying the age dependence of birth and death processes. The fate of various age categories is drawn as cohort survivorship curves in Fig. 4. Juveniles carry the greatest risk in the wet meadow 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. In all, this is a Deevey type III sur-

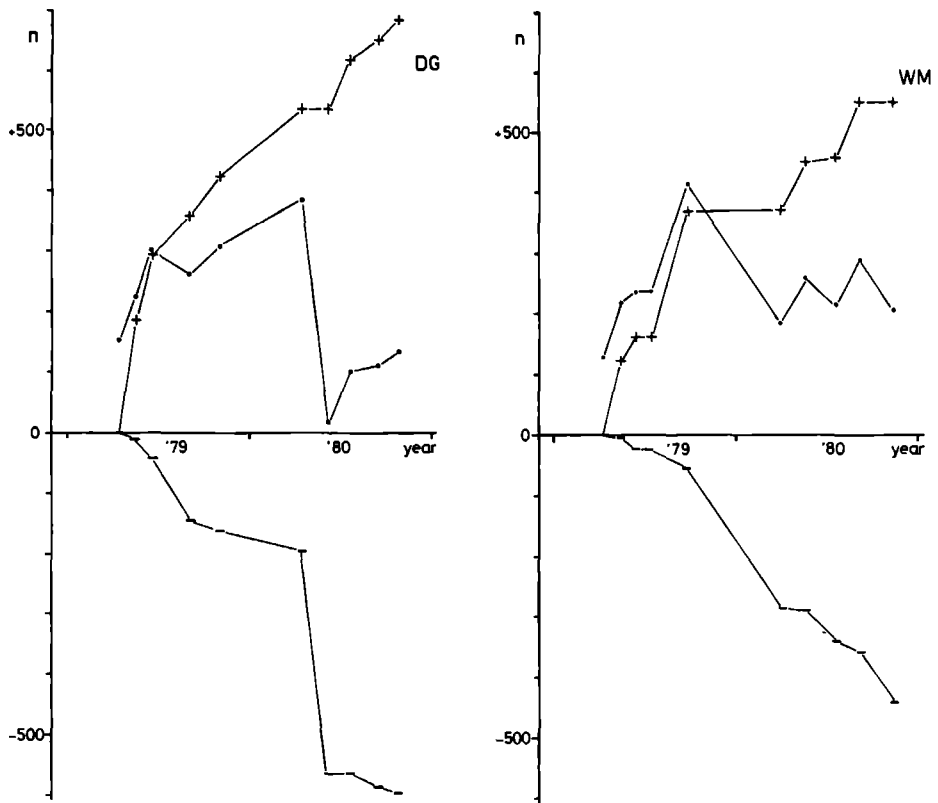


Figure 3. Total number of rosettes of *Plantago lanceolata* over time present in 0.375 m^2 in a dry dune grassland (DG) and in a wet meadow (WM). Cumulative numbers of rosettes that were born (+) and that died (-) are presented as well.

vivorship curve. 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 in a separate chapter.

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 ef-

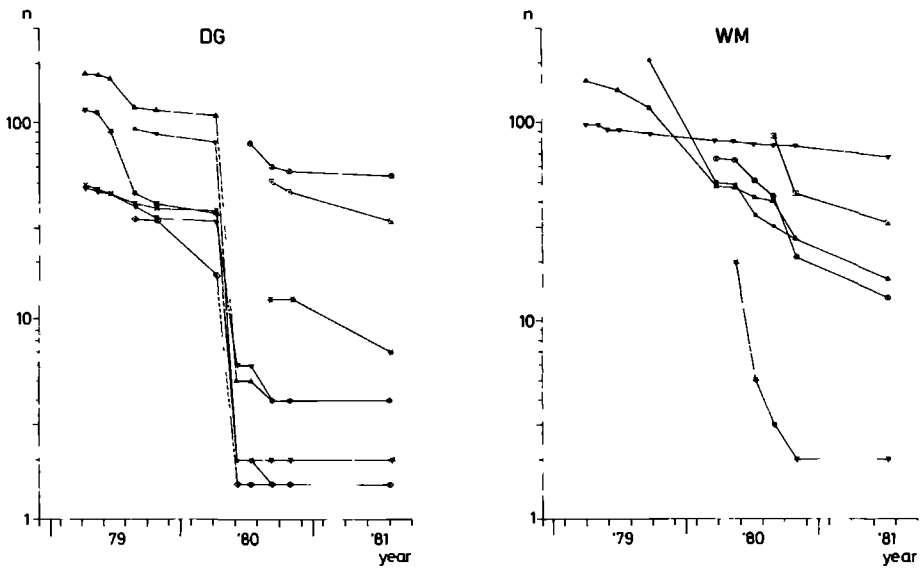


Figure 4. Survivorship curves for various cohorts of *Plantago lanceolata* from a dry dune grassland (DG) or from a wet meadow (WM). Symbols are as follows: ▲ spring cohort of seedlings 1979; ● autumn cohort of seedlings 1979; ★ spring cohort of side rosettes 1979; ◆ autumn cohort of side rosettes 1979; ▼ 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.

fect 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 and the whole survivorship curve is much more that of a Deevey type II. Plants can flower the second season after germination. The cohort carrying the greatest risks is that of side rosettes, but nevertheless they have a profound 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 cannot be established.

Although it is clear that there are important differences in age-dependent survival and time to adulthood, these differences have their greatest effect early in life. Therefore, size is a relatively more important criterium in the demography of these plants as has been stressed by Werner & Caswell (1977).

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 x 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

The effect of size on reproductive effort, survival, side rosette formation and herbivore damage is also apparent from a comparison between the two ecotypes (Table 1 and 2). Reproduction starts at smaller sizes in the dry population, more plants per category do flower and there is a stronger correlation between size and reproductive output. Once committed to flowering, plants in the wet site produce a rather constant number of ears. The reproductive output 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 smallest category in the wet meadow and in the larger categories in the dune grassland. This is the result of the difference 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

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 x 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

but there is a surprisingly high predation on the tall inflorescences in the hay meadow, which are eaten mainly by birds such as wood pigeons, ducks and pheasants.

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 adulthood and the number of times the plant can be expected to flower, but also in the percentage of adults flowering and the amount and 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 120 seeds are produced as an average per genet. In the wet meadow this is about 108 seeds, produced by a few big spikes in late spring. Taking the lifespan of individuals into account, however, more seeds are produced in the wet site per adult. 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 iterocarp, which state that the most pronounced iterocarp should

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

	dry grassland			wet meadow		
	n	mean	CV%	n	mean	CV%
Number of leaves	53	8.0	27	35	5.7	25
Length of longest leaf cm	53	34	24	35	203	24
Number of ears/rosette	53	3.8	45	35	1.8	47
Number of ears/genet	32	9.2	69	35	1.7	47
Length of scape cm	53	5.4	61	35	38.0	29
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
Seeds/mm of spike	30	1.7	69	30	2.5	29
Weight/seed mg	30	0.7	75	30	1.9	39

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). 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 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 iterocarpny in the genus *Plantago*. The relationship between number of seeds and reproductive effort shows that in the wet meadow more seeds are produced at considerably

Estimated number of seeds
per rosette

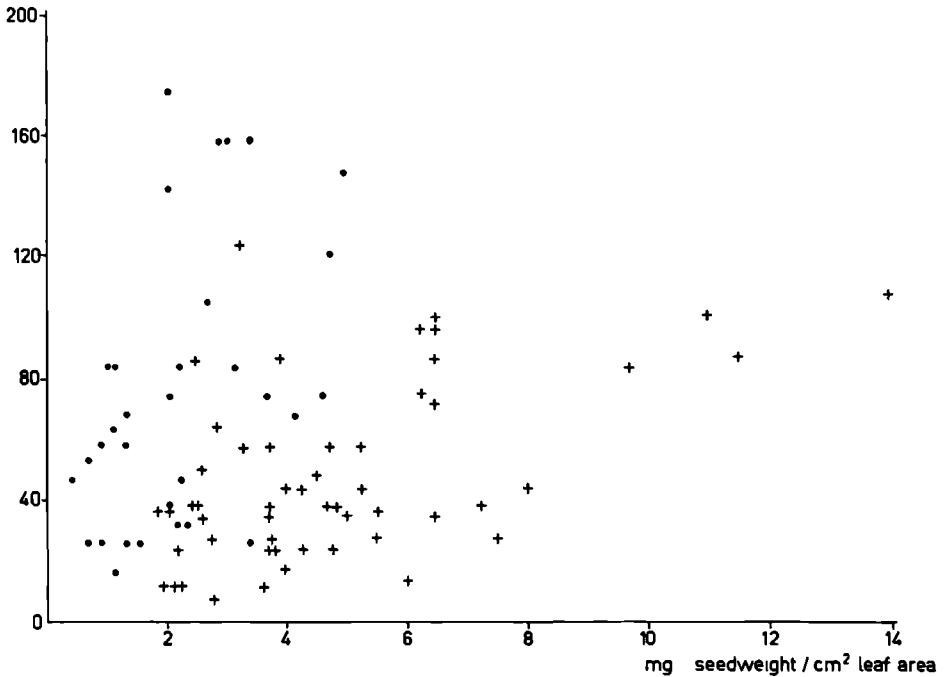


Figure 5. Estimated number of seeds per rosette of *Plantago lanceolata* from a dry dune grassland (+) or from a wet meadow (•) as a function of reproductive effort, expressed as mg seed weight produced per cm² of leaf area.

lower costs than in the dry 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 iterocarpic, is the relationship between

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 cm² 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 x length of longest leaf).

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

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 15 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 two ecotypes of *Plantago lanceolata* in an evolutionary context as selection for reduced iterocarp.

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 to 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

CONCLUSIONS

The complete demographic profile for the two populations of *Plantago lanceolata* presented in this paper shows clear contrasts that seem to be related to the environmental conditions where they are found.

The population in the dry dune grassland is under strong abiotic control. The soil is poor in nutrients and there is frequently a shortage of water, which sometimes takes the shape of catastrophic droughts. An important biotic factor is grazing by cattle. The population is short-lived with a more or less Deevey type II survivorship curve, indicating that juveniles and adults carry about equal risks of dying. There is only a short juvenile period and plants flower the second season. Seed production itself shows a clear size dependence and is found in small as well as in big rosettes. Many side rosettes are formed, which have a high probability of dying, but which, when successful, can flower in the same season as they were born. Seeds are produced from many short inflorescences which arise from the axillary meristems in the many short leaves that constitute a rosette in this habitat. Seeds are produced at great costs. Within one spike a limited amount of resources are distributed over the embryos 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 of which 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 forms a strong contrast with the population from the dry dunes. The soil in the wet meadow is completely organic and relatively well supplied with nutrients. The watertable is always at or shortly below the soil surface. The population is 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. This results in distinctly hollow Deevey type III survivorship curves. 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 from the axils of the few leaves that form one rosette. A large number of big seeds can be filled on one spike 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 seed produced. The reproductive effort affects to some extent the reproductive success in the future. These two observations are consistent with conditions that in theory favour iterocarp. The seeds have only a 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, long-lived, iterocarpic perennial adapted to live in stable environments.

The relations between the demographic features of the two populations of *Plantago lanceolata* and the habitat characteristics strongly suggest that there is local adaptation and that both populations have undergone natural selection towards the different life histories demonstrated in this paper. However, the intuitive fit between habitat and life history constitutes insufficient grounds for such a conclusion. Independent proof is necessary to establish the adaptive significance of the differences observed in the two plantain populations (Van Groenendael, 1985b,c).

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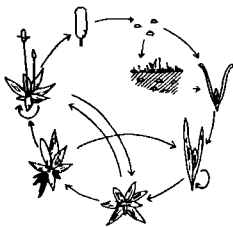
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This chapter is written together with P. Slim and submitted for publication.

THE CONTRASTING DYNAMICS OF
TWO POPULATIONS OF *PLANTAGO LANCEOLATA* L.,
CLASSIFIED BY AGE AND SIZE

SUMMARY

The dynamics of the two populations of *Plantago lanceolata* L. are simulated with the use of matrix projection models. The fecundity and survival parameters that together form the matrix, are based on demographic fieldwork and evaluated for both size and age categories at the same time, using the formulation originally proposed by Goodman. The output of the model is verified against field data and this proved to be satisfactory. After verification sensitivity analysis is applied to the model to find the life history traits that are most important in defining the population growth rate. Both absolute and relative perturbations are used in this analysis and their biological implications are discussed. The results from the analysis are in general agreement with expectations based on field experience: new recruitment is most important in the population from an unpredictable environment, whereas adult survival is most important in the population from a stable environment. In an evolutionary context, on the basis of Fisher's theorem, the calculated sensitivities can be used to predict selective pressures on life history traits. Some pitfalls in this approach are discussed. The particular form of the matrix projection model in this paper is time-invariant. However, fecundity and survival rarely are constant over time. Therefore random sequences of good, normal and bad years are generated and incorporated in the model. The impact of various proportions of good, normal and bad years on the model is evaluated, using time to extinction as a measure. In a final section the use of matrix projection models for purposes of description and prediction are listed and discussed.

Since their first formulation by Lewis (1942) and Leslie (1945) matrix projection models have been given much attention in population biology. Useful demographic properties can be obtained from solving the characteristic equation, either analytically or numerically. Many extensions have been proposed to the original model, according to the specific needs of the user (Usher, 1972). In the original form matrix elements describe survivorship and fertility schedules, based on age categories, but other categories can be used as well (Lefkovitch, 1965) or even combinations of categories (Goodman, 1969; Law, 1983). Matrix models can be made stochastic (Pollard, 1966; Boyce, 1977; Tuljapurkar, 1982) or functions of harvesting or density (Usher, 1972) and arranged in ways so that even quite complex life histories can be modelled (Caswell, 1982). This all shows the wide applicability of the matrix formulation for modelling populations and simulating the various effects of changes in the parameters of the model.

Apart from its use in a demographical sense, the model is also used in life history theory. This stems from the fact that the population growth rate can be used as a measure of fitness (Fisher, 1958; Emlen, 1973). Especially since Caswell (1978) developed a general formula for the simultaneous calculation of the effect of small changes in each parameter of the model on this growth rate, it has become possible to compare directly the relative effects on fitness of various life history traits, even in non stable or variable environments (Templeton, 1980; Tuljapurkar, 1982). This in turn can lead to hypotheses concerning the heritability of those traits along lines suggested by Stearns (1977, 1980) and recently by Schmidt & Lawlor (1983).

It is the aim of this paper to apply the matrix formulation to describe the complex life history of two ecotypes of *Plantago lanceolata* from contrasting habitats, incorporating seedbank, vegetative ramification, seasonality and senescence, based on demographic data (Van Groenendael, 1985b). After verification of the model against the field data, it will be evaluated by means of sensitivity analysis and used in simulating the effects of variation in environmental conditions like stochastic disastrous droughts, known to be important in the field. By using two ecotypes that are proven to be genetically different for various life history traits, it must be possible to confront the evolutionary predictions of the model with experience from the field. Further experimental tests are presented elsewhere (Van Groenendael, 1985b,c).

The populations

The first of the two ecotypes is found in a dry dune grassland (DG), grazed as a commonage for over three centuries by cattle and horses. The soil is sandy and low in nutrients (Troelstra, 1978), sometimes experiencing unpredictable and catastrophic droughts. The individuals are small, short lived, with many prostrate leaves and inflorescences, bearing short ears on short scapes. Flowering and setting of seed takes place between June and September. The seeds are small and form a substantial seedbank. Main germination is in spring and plants grow quickly, so that they can flower in the next season. Formation of side rosettes is abundant.

The other population is found in a wet hay meadow (WM), situated in an old filled-in riverbed, mown once a year in mid-July. The soil is a completely organic peat, that is permanently waterlogged and rather productive. The individuals of *Plantago lanceolata* that grow here are tall with few tall erect leaves and inflorescences, bearing long spikes on long scapes. They flower in May and produce big seeds in June and July that form no seedbank to speak of. Main germination is in autumn and plants grow very slowly. It takes at least three years before they flower. Only very seldomly side rosettes are formed in the field, and individuals are rather long lived. The main demographic features of both populations based on field observations over the period of 1979-1981 are summarized in Table 1.

The model

In building a matrix projection model much depends on the initial choice of categories and time steps, for which the transition probabilities and fecundity will be evaluated. Although Werner & Caswell (1977) quite convincingly argue that a stage projection matrix is superior to a matrix based on age this might be less true for a definitely iterocarpic perennial with age dependent fecundity, age dependent seed decay in a seedbank and senescence in old age. Therefore the model, proposed by Law (1983) was preferred, because it uses age and size categories simultaneously. Considerable modifications were necessary, however, to accommodate the complex life histories of the two *Plantago* populations (Van Groenendael, 1985b).

Table 1. Characteristic differences between two populations of *Plantago lanceolata* from a dry dune grassland (DG) and a wet meadow (WM), respectively.

	dry grassland (DG)		wet meadow (WM)	
	mean	CV%	mean	CV%
No. of leaves	6.6	27	3.8	25
Length of longest leaf mm	34	24	203	24
No. of ears	9.2	69	1.7	47
Length of scape mm	54	61	380	29
Length of ear mm	7.3	31	17.1	34
No. of seeds/ear	15.74	75	57.21	53
Seed-weight mg	0.73	75	1.91	39
No. of side rosettes	3.6		0	
% adults flowering	31		20	
% rosettes with side rosettes	12		0	
No. of seeds in the soil per m ²	1700		500	
No. of seedlings per m ² 1979	779		1158	
1980	486		465	
% germination in spring 1979	68		44	
1980	75		46	
% seedlings surviving 1979 → 1980	59		26	
1980 → 1981	45		28	
Half-life adults in months	20		46	

The individuals in a Goodman matrix (Law, 1983) are categorized by age, before they are placed in a size category. This results in small size matrices as elements of a larger age matrix. Time is divided in years and size is based on a non-destructive estimate for biomass. This estimate is based on the number of leaves, times length of longest leaf in cm and has a good correlation with biomass (Noë & Blom, 1981). Five equal size categories have been created after a log transformation to the basis of two. This results in a roughly even distribution of individuals over size categories, necessary to avoid distortion in the estimation of the transition probabilities between size categories. It introduces, however, an increasing robustness in the larger size classes for any

B ₁	.	.	B _{2a}	B _{2s}	B _{2z}	B ₃	B _{3z}	B ₄	B _{4z}	B ₅	B ₆	N _{1a}
.	B ₁	.	B _{2a}	B _{2s}	B _{2z}	B ₃	B _{3z}	B ₄	B _{4z}	B ₅	B ₆	N _{1s}
.	.	.	Z ₂	Z ₂	.	Z ₃	Z ₃	Z ₄	Z ₄	Z ₅	Z ₆	N _{1z}
P _{1a}	N _{2a}
.	P _{1s}	N _{2s}
.	.	P _{1z}	N _{2z}
.	.	.	P _{2a}	P _{2s}	N ₃
.	P _{2z}	N _{3z}
.	P ₃	N ₄
.	P _{3z}	N _{4z}
.	P ₄	P _{4z}	.	.	N ₅
.	P ₅	.	.	N ₆

Figure 1. A 12 x 12 Goodman matrix for a population of *Plantago lanceolata* from a dry dune grassland and the 1 x 12 stage vector belonging to it. Elements are arranged in six age categories and each element contains five size classes, as a 5 x 1 (B, Z) 1 x 5 (N) or 5 x 5 (P) matrix, not shown. B = number of seedlings produced per age class. Z = number of side rosettes produced per age class. P = transition probabilities between age classes. N = number of individuals per age class. a = autumn cohort, s = spring cohort, z = cohort of side rosettes. (for further explanation see text).

parameter, that has a more or less linear relationship with size (seed production for instance).

Sorting procedures on the demographical data collected over three years provided the numbers in each category from which the transition probabilities could be calculated from year to year, using the first of July as the census date. This is the moment after which the seeds are released from the parent rosette. The parameter values differ from year to year, but for the model the maximum values have been chosen, in order to arrive at the most 'optimistic' life history. For simulation of the effects of changes in parameter values, the range over time has been taken into account.

The following basic assumptions have been made in constructing the model:

ties. The same holds for cohorts of side rosettes. During the course of time these initial differences disappear and the cohorts are merged by putting the relevant transition matrices next to each other on the same row (Fig. 1 and 2).

- Autumn and spring cohorts of seedlings are recruited separately into the population according to their relative proportion, using two separate rows of matrices. Together they represent the total seed production. Recruitment via side rosettes, if occurring, forms a third row. Because side rosettes are mainly formed in spring there is no seasonal difference there.
- The fecundity matrices summarize a series of sequential steps, starting with the proportion of individuals that flower in each age/size category, the mean production of seeds per flowering individual in that category, seed predation per category and the proportion of seeds that germinate. The establishment of seedlings is incorporated in the first transition matrix to avoid further cumulation. This is in contrast to Law (1983) who included this survival to the next census date in the fecundity element.
- The seedbank in the dry population is represented by two matrices on the diagonal in the upper left hand corner (Fig. 1). This is as much as defining the capacity of seedlings to produce seedlings the next census. This is equivalent with saying that each seed crop produces a certain percentage of its seedlings one census later. These again produce seedlings yet another census later and by the same percentage, modelling this way the effect of a seedbank with a constant decay rate. Because seedlings are all in the same age and size category, these two matrices consist of one single figure, being this decay rate.
- The demographic information has been gathered over a three year period. By carefully partitioning the initial population in three sections - seedlings, non flowering juveniles and flowering adults - and following these over time, it is possible to estimate the fate of the population over a longer period by assuming that these three cohorts are sequential rather than co-occurring, combining static and dynamic life table data. As far as different cohorts are assembled this approach works under the assumption of stable age/size distribution.

The numerical values given to all parameters in the model are presented in an appendix.

RESULTS

Limit properties

The resulting matrices have been solved numerically by iterative multiplication of the projection matrix with a stage vector, until the difference between subsequent values of λ being the dominant eigenvalue was smaller than 10^{-4} . The solution is more or less independent of the values in the stage vector, as long as there is a greater than zero expectation for reproduction (Law, 1983). In practice the stage vector contained values for autumn and spring cohorts of seedlings only (N_{1a} and N_{1s}) all placed in the smallest size

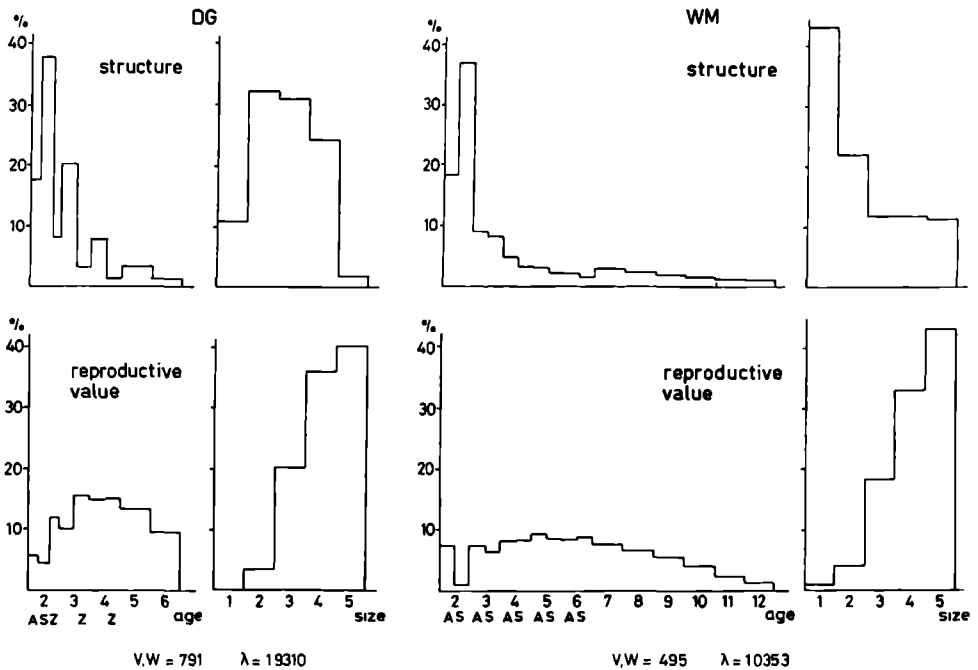


Figure 3. Limit properties of the Goodman matrices for two populations of *Plantago lanceolata* from a dry dune grassland (DG) and a wet hay meadow (WM) respectively. Stable age and size structures from the right eigenvector V are drawn and the stable age and size distributions of reproductive values from the left eigenvector W . The scalar product of the eigenvectors, indicating the mean length of generation and the dominant eigenvalue, representing the population growth rate λ , are presented as well.

category. By arranging the stage vector as a column vector and premultiplying this with the projection matrix one obtains after iteration the right eigenvector V representing the stable age/size distribution. By arranging the stage vector as a row vector and postmultiplying this vector with the projection matrix, one obtains the left eigenvector W , representing the reproductive values given age and size. The scalar product of both eigenvectors $\langle V, W \rangle$ is a measure for the mean length of generation (Leslie, 1966). The year to year increase in numbers of individuals is the population growth rate λ , equivalent to the dominant or maximum eigenvalue. The dry population (DG) is stable after 22 iterations at $\lambda = 1.9310$ and the wet population (WM) is stable after 79 iterations at $\lambda = 1.0353$. These limit properties, standardized and expressed as percentages are presented in Fig. 3. Note the unexpectedly low mean length of generation for the wet meadow population, in which the adults are long-lived but seeds and seedlings very much at risk, resulting in this low value.

Verification and interpretation of the model

The actual age and size distributions and survivorship curves for various cohorts of seedlings and side rosettes are compared with those calculated in the model. Fig. 4 shows the survivorship curves for the dry (DG) and the wet (WM) population, respectively. The actual data are given in Van Groenendael (1985b). The calculated survivorship curves are arrived at by setting all B and Z elements equal to zero and filling N_{1a} , N_{1s} or N_{1z} with 1000 individuals each and recording their fate over time using the same iterative multiplication as outlined above. Because the dry population (DG) suffered from a catastrophic drought in the second year, only survivorship over one year of the various cohorts in the field is available. These show almost equal slopes between seedling cohorts and adult cohort suggesting straight Deevey type II depletion, except for the side rosettes that suffer greater initial mortality. The calculated lines have almost exactly the same slopes, although slightly less steep. In the wet population the spring and autumn cohorts of seedlings follow closely the calculated survivorship curve, which is distinctly hollow (Deevey type III). The calculated autumn cohort reaches a steady slope after six years, the spring cohort after 5 years, both having more or less the same slope, which is equal to the decline of adults in the field.

Comparison between real and calculated size and age distributions gave a satisfactory fit between calculated stable age and size distributions and

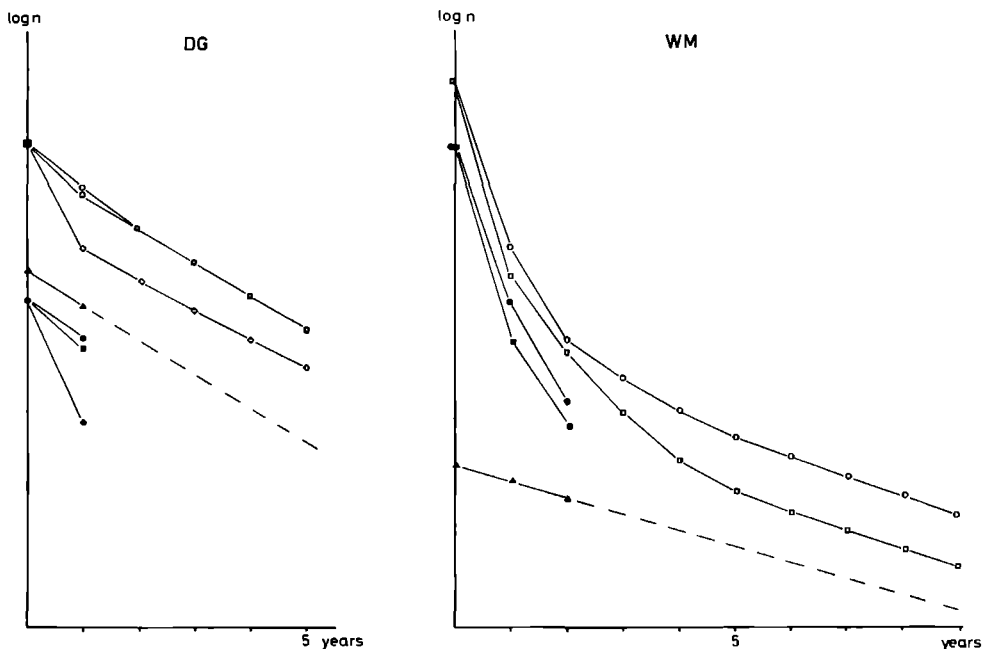


Figure 4. Real and calculated (open symbols) survivorship curves for various cohorts of *Plantago lanceolata* from a dry grassland (DG) and a wet meadow (WM). ● ◯ spring cohort of seedlings; ■ □ autumn cohort of seedlings; ◆ ◇ cohort of side rosettes; ▲ adults.

field observations (Fig. 5). Size distributions give a somewhat less satisfactory fit than age distributions, understandable from the more variable nature of size and the dry population shows less similarity than the wet population, but the differences are not significant in a χ^2 -analysis.

After having established the trustworthiness of the created models, it is possible to discuss with more confidence the biological implications of the limit properties of these matrix models. Given the fact that all parameters have been chosen optimally, it is clear that the dry population can grow much faster and reaches model stability much faster (has a greater resilience) than the wet population, which is in agreement with the more unpredictable hazardous conditions in the dry dune grassland, when compared with the more stable conditions in the wet hay meadow. Juveniles and adults are equally at risk in the dry population, whereas young plants suffer greater mortality in the wet site. This latter condition should favour iterocarpny according to Charnov &

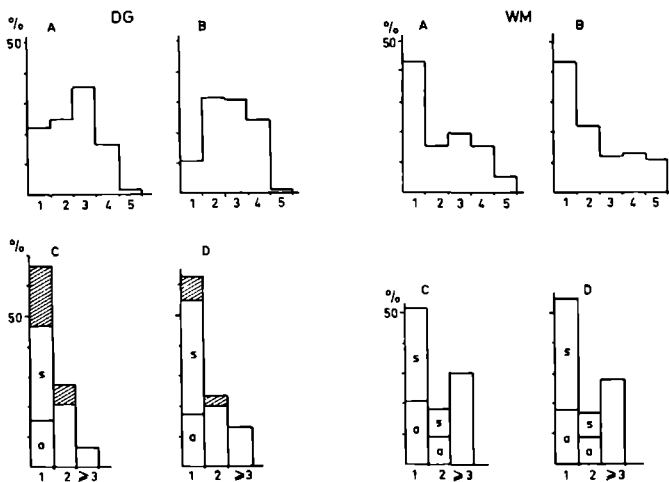


Figure 5. Observed (A, C) and calculated (B, D) size and age distributions (top row and bottom row respectively) for two populations of *Plantago lanceolata* from a dry grassland (DG) and a wet meadow (WM). Autumn (a) and spring (s) cohorts as well as side rosettes (hatched) are indicated in the age distributions. χ^2 -values for the comparison between observed and calculated frequencies were all not significant. A - B : 6,84 and 1,81; C - D : 2,67 and 0,18 for DG and WM.

Schaffer (1973) and this is confirmed in this case. The size hierarchy in the wet site is more skewed to the left, indicating stronger competitive effects (Harper, 1967, 1977), which again is quite likely, given the more productive and dense vegetation in the wet meadow. Reproductive values reach their maximum in the third year in the dry site, but the side rosettes have very high reproductive values right from the beginning. They are an essential part in the life history of this population. The population from the hay meadow has a less marked peak in reproductive value at the fourth year. As expected, size has a pronounced effect on reproductive value, but there is more reward for growing big in the wet site than there is in the dry site.

Sensitivity analysis

A further use of the model can be made by testing the sensitivity of the population growth rate for small changes in model parameters (Caswell, 1978). For

all parameters this can be achieved by multiplying left and right eigenvector, which results in a matrix in the form of the original matrix, but with all non zero matrix elements replaced by their sensitivity. The formula of Caswell's sensitivity measure reads:

$$\frac{d\lambda}{da_{ij}} = \frac{V_i W_j}{\langle V, W \rangle}$$

Apart from the comprehensive insight in the functioning of the model, a sensitivity analysis is less dependent on the exact values of the model parameters, as long as their relative proportions are more or less accurate. It can therefore be applied, even when the model itself is not very precise, to get an idea what the important moments are in the life history of a population.

In both populations the establishment of new rosettes from seed or as side rosettes is the most important phase in their survival, as indicated by the summed sensitivities of all P_{ij} elements in Figs. 6 and 7. Establishment, how-

B_1		B_{2a}	B_{2e}	B_{2z}	B_3	B_{3z}	B_4	B_{4z}	B_5	B_6	Σ
100		4	6	13	24	5	13	2	6	2	176
(5)		(7)	(1)	(7)	(22)	(11)	(20)	(6)	(15)	(6)	(100)
	B_1	B_{2a}	B_{2e}	B_{2z}	B_3	B_{3z}	B_4	B_{4z}	B_5	B_6	
	168	1	5	11	20	5	10	2	5	2	233
	(9)	(11)	(2)	(12)	(37)	(19)	(34)	(11)	(25)	(11)	(169)
		Z_2	Z_2		Z_3	Z_3	Z_4	Z_4	Z_5	Z_6	
		33	68		39	6	15	2	7	3	173
		(3)	(9)		(36)	(8)	(17)	(3)	(9)	(3)	(87)
P_{1a}											
1456											1456
(83)											(83)
	P_{1z}										
	2106										2106
	(156)										(156)
		P_{1z}									
		2369									2369
		(87)									(87)
			P_{2a}	P_{2e}							
			541	1035							1577
			(74)	(148)							(222)
					P_{2z}						
					447						447
					(68)						(68)
						P_3					
						765					765
						(128)					(128)
							P_{3z}				
							101				101
							(46)				(46)
								P_4	P_{4z}		
								331	71		402
								(57)	(11)		(68)
										P_5	
										132	132
										(20)	(20)
											Σ 9935
											(1238)

Figure 6. Sensitivities x 100 of the population growth rate for small absolute and relative perturbations (between brackets) in the matrix elements of a population of *Plantago lanceolata* from a dry dune grassland.

ever, is more important in the wet meadow especially from seedlings that have germinated in the autumn. After establishment survival of juveniles (P_2 elements) and of adults (remaining P elements) remains more important in the wet hay meadow. Fecundity on the other hand, is more important in the dry dune grassland (Bele-

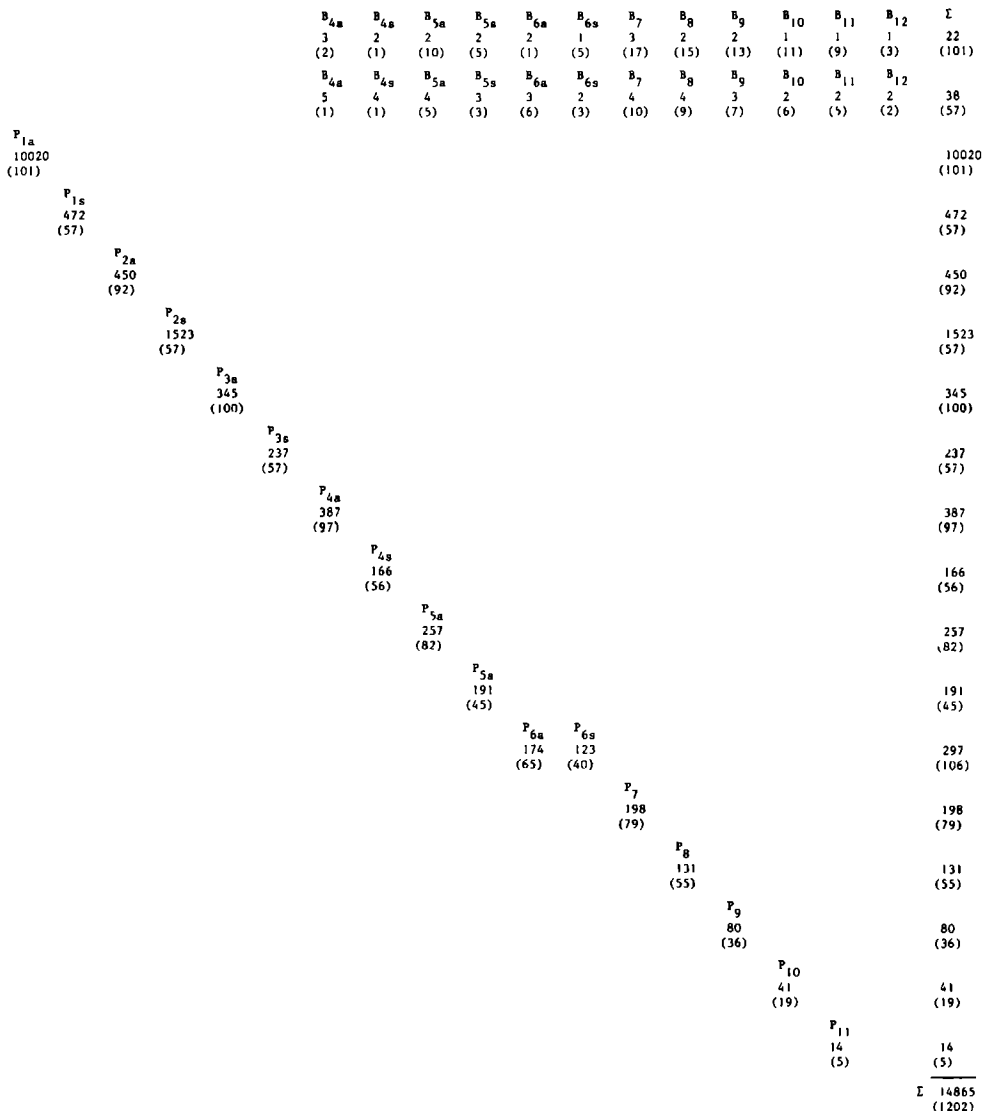


Figure 7. Sensitivities x 100 of the population growth rate for small absolute and relative perturbations (between brackets) in the matrix elements, of a population of *Plantago lanceolata* from a wet hay meadow.

ments), mainly in three and four year old rosettes. Side rosettes have an important function especially when formed in relatively young parent rosettes (Z_2 and Z_3). Their importance is that they enlarge the capacity of a rosette to produce seeds. This is reflected in the relatively high sensitivities for seed production in young side rosettes (B_{2z}). Not shown in Figs. 6 and 7 are the effects of size, but the fastest growing seedlings are important for establishment (P_1) and juvenile survival (P_2). Fecundity depends on small plants in the beginning, but this shifts to larger plants later on.

In inspecting the results of the sensitivity analysis, one of the first points that attracts the attention, is the relative unimportance of seed production, a fact also noted by others (Caswell, 1978; Caswell & Werner, 1978). In the two cases at hand this applies to all B and Z elements, that is all elements not expressed as a (small) chance but as a (large) number. Apparently small but absolute perturbations have a large impact when the transition probabilities are small and only a weak effect on the much larger fecundity elements. By calculating the effect of small relative perturbations by multiplying the right hand side of the sensitivity equation with the actual parameter values a_{ij} , this can be avoided (De Kroon et al., submitted). Subsequent standardization for the different population growth rates makes the relative sensitivities directly comparable between the two populations (Figs. 6 and 7). The absolute sensitivity measures the effect of absolute shifts in life history parameters, whereas the relative sensitivity takes into account the actual life history realized in the field. This can be demonstrated by looking at recruitment. In an absolute sense the summed sensitivities of recruitment, excluding the seedbank (B_1) show that both populations are most sensitive to recruitment into the 'wrong' cohort, that is, the cohort that is least important in the field. Although both results seem puzzling at first sight, there are biological explanations. In the wet meadow the fewer spring seedlings have better chances than autumn seedlings, but the loss of seed over winter is greater than the loss of seedlings over winter. Only 20% of the seeds germinate, whereas about 33% of the seedlings survive to the next census, so that it might be better to face the risk of dying in winter time as a seedling rather than as a seed. Mortality over winter is very low in the dry site, so that there is no apparent advantage in postponing germination, but here the major factor could be that there are good reasons to produce seeds later in the season, as is the case, after the spring and early summer droughts. Seeds have a clear pattern of dormancy necessary to form a seedbank but also preventing autumn germina-

tion and this results in a great spring flush of seedlings. These biological constraints are implicit in the relative sensitivities and these do show the correct pattern of recruitment, as well as less extreme contrasts between survival and fecundity elements.

Simulations

Instead of calculating from a sensitivity matrix the effect of complex changes in the life history by adding the appropriate sensitivities, it might be easier to simulate such changes. This is especially true, when matrix elements are added or removed or when the dimensions of the matrix are changed. A series of such simulations have been executed, based on biologically interesting 'what, if ...' questions (Table 2). Direct comparison between various changes in the

Table 2. Simulated population growth rates, expressed as a proportion of the original growth rate for various complex changes in the life histories of two populations of *Plantago lanceolata* from a dry grassland (DG) and a wet meadow (WM) respectively.

	DG	WM
Germination mainly in spring	1.0000	1.0340
Germination mainly in autumn	1.0125	1.0000
All germination in spring	0.9880	1.0486
All germination in autumn	1.0254	0.9791
Seed production independent from age	1.2234	1.0114
Seed production one year earlier	-----	1.0146
Seed production one year later	0.9839	0.9833
Life one year shorter	0.9830	0.9892
Seed production without seed predation	1.0260	1.0402
Seed production with double seed predation	0.9713	0.9447
No seedbank	0.9890	-----
Half-life of seedbank x 2	1.0115	-----
Recruitment only via side rosettes	0.7695	-----
Recruitment only via seeds	0.9145	-----
All recruitment x 0.5	0.8306	0.9161
All survival probabilities x 0.5	0.6156	0.5482

life histories of the two ecotypes now becomes much easier. Postponing reproduction one year or shortening life with one year reduces the population growth rate about equal amounts in both populations, notwithstanding the different generation times. This is the result of the much steeper rise and fall in reproductive value over time in the dry site that in the wet site, also apparent when seed production is made independent from age. In general new recruitment is much more important in the dry site, whereas survival is more important in the wet site. When recruitment in the dry site is splitted over the various ways new recruits can be produced, direct germination is the most important source. Seedbank has a relatively low impact. Loss through seed predation is more important in the ungrazed wet meadow than in the grazed dry grassland. A flowering rosette in the wet meadow contains only one or two long stalked inflorescences. The main seed predation is by birds taking complete ears, reducing seed production very severely. Apparently the necessity for partitioning the reproductive effort in few 'high investment' inflorescences must be more important than the unpredictable risk of seed predation. This risk is avoided in the dry site with its many short ears on short stalks, and its long history of grazing.

Effect of stochastic fluctuations

The model might produce realistic survivorship curves and age/size distributions, it is still quite unrealistic in exhibiting exponential growth and having constant (optimal) values for the model parameters. These values will differ locally and in time. The resulting variability has a pronounced effect on the population growth rate (Boyce, 1977; Tuljapurkar, 1982). According to Tuljapurkar (1982) the effect of a certain variance in a parameter is proportional to its sensitivity squared, the sensitivity calculated according to Caswell (1978). The result could be that an otherwise less important parameter in a static model because of a large variance could have a greater effect on λ in a probabilistic model than a parameter with a greater sensitivity in such a static model. This risk is most pronounced when the overall level of the sensitivities is low (Tuljapurkar, 1982) as is the case in the population from the wet meadow. This predicts a much lower resilience for this stable population than for the less stable population from the dry dune grassland. The consequence from an evolutionary point of view could be that not only the level of a trait that has a great effect on λ will be under selective pressure but

also the variability when such a variability happens to have an important effect on λ . The first could result in low levels of genetic variability, the second in low levels of plasticity (Van Groenendael, 1985b).

A fully stochastic model, although quite feasible mathematically is hardly possible on the basis of the field data. However, because field data have been gathered over a three year period, there is at least some information on the variability over time. To get some idea of the effects of this variability the following numerical procedure has been adopted: The year with lowest parameter values over the three year period has been chosen to represent a bad year. A good year has the actual values in the model. The remaining year represents a normal year. By applying a reduction factor on the actual matrix elements these three environmental states are created. Although this factor could work on specific entries in the matrix, simulating specific effects of bad years, in this case a more robust approach is chosen. The factor affects all B + Z elements and/or all P elements. In the dry dune grassland a bad year influences survival as well as seed production. Because a bad year means a period of summer drought some seed production is supposed to have taken place, so that there is a lesser reduction for seed production than for survival. In the wet meadow bad years only affect seed production. There is hardly any effect on survival. The actual factor values are listed in Table 3.

Table 3. Reduction factors on various matrix elements, representing good, bad and normal years in both populations. Factor values are based on field observations.

	DG			WM		
	bad	normal	good	bad	normal	good
B + Z elements	0.30	0.75	1.00	0.30	0.60	1.00
P elements	0.05	0.75	1.00	1.00	1.00	1.00

A random sequence of good, bad and normal years is generated in proportions fixed beforehand. To evaluate the impact of a certain set of conditions, the population growth rate is no longer a useful measure. It is replaced by time to extinction, which is considered equivalent with or even superior to the

population growth rate as a measure of fitness (Cooper, 1984). The model is run using the stable age/size distribution as the initial stage vector and an arbitrary but low extinction threshold after which the run stops. This was repeated several times (30) to get an estimate of the number of years in which the population goes extinct given a particular proportion of good, bad and normal years with a given set of reduction factors.

In order to get extinction, the proportion of bad years always had to exceed the good years resulting in crude but definitely skew distributions of para-

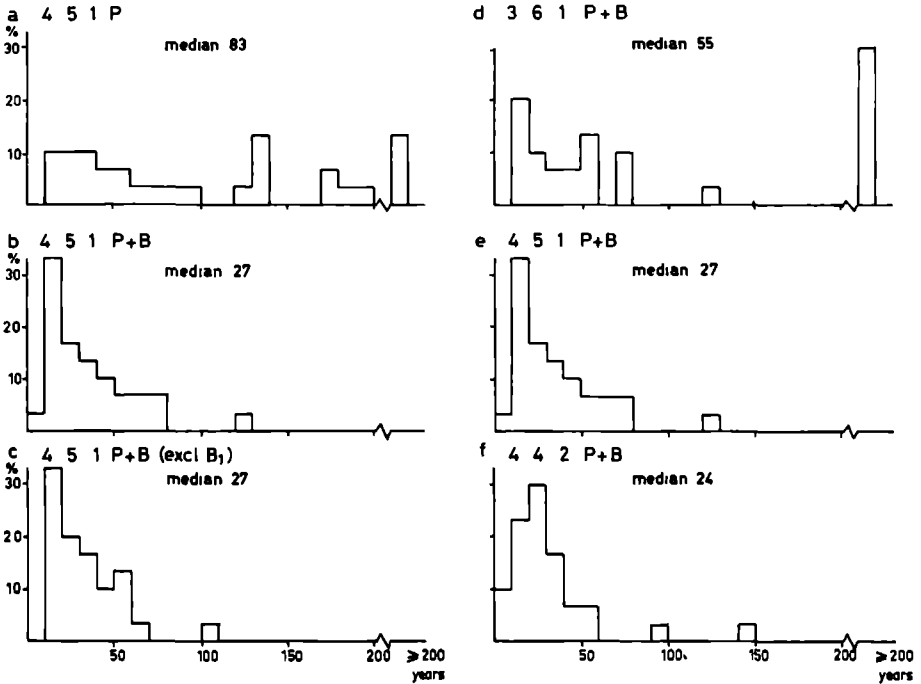


Figure 8. Frequency distributions for time to extinction based on 30 simulation runs, given stochastic combinations of bad, normal and good years in various fixed proportions (a - f), affecting the survival (P) and/or the fecundity (B) elements in a matrix projection model of a population of *Plantago lanceolata* from a dry dune grassland. The strength of the reduction factors is given in Table 3.

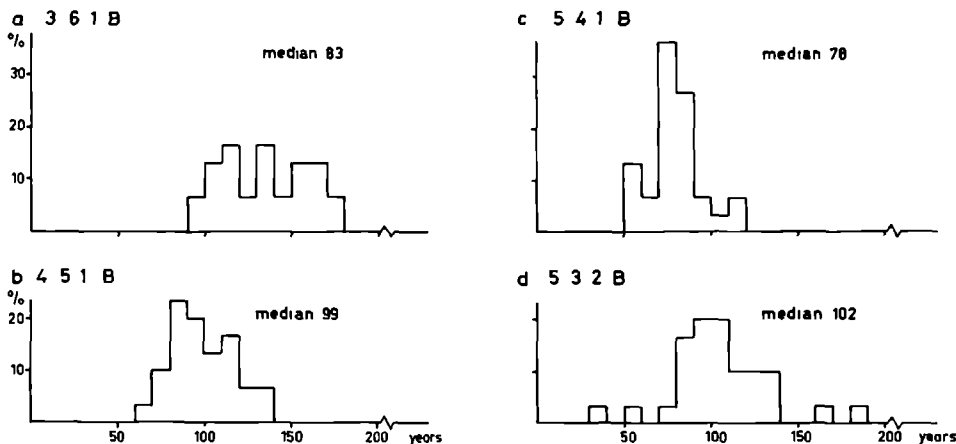


Figure 9. Frequency distributions for time to extinction based on 30 simulation runs, given stochastic combinations of bad, normal and good years in various fixed proportions (a - d), affecting the fecundity (B) elements in a matrix projection model of a population of *Plantago lanceolata* from a wet meadow. The strength of the reduction factors is given in Table 3.

meter values. Biologically this makes sense as there are fewer chances for a good year to occur because all circumstances that influence survival and/or seed production have to be optimal. The chance for a bad year to occur is much greater, because it can be achieved in various ways resulting in skew distributions. This distribution has a profound influence on the time to extinction as shown in Figs. 8 and 9. Time to extinction first of all depends on the level of the parameter values, represented by the population growth rate. When the population growth rate is high, strong effects are necessary to cause extinction (Fig. 8) and there is a strong skewing in extinction times. It also depends on the variance and the skewing in the parameter values. The general picture of these simulations is that the population from the stable wet meadow has a narrow and more or less normal distribution of extinction times and therefore very little possibility to escape extinction through chance. The population from the dry dune grassland has a much better chance to survive the hazards of life.

There is no doubt about the general usefulness of matrix models in describing the dynamics of populations of (plant) species, even with quite complex life histories. Large data sets can be condensed and evaluated by means of few demographic key parameters that are easily calculated from the model. In the population from the wet site, juveniles carry a greater risk than adults when compared with the population from the dry site, maturation is delayed, iterocarp is more pronounced, there is a lower reproductive effort and larger seeds, the population is more or less in a steady state in this habitat, that is stable and predictable except for the risk of predation. All these characteristics are reversed in the dry site, presenting an almost ideal contrast, but all these observations could have been done without the help of a model. Strictly speaking this is not true for the estimated growth rates, stable age/size distributions and the distribution of reproductive values, but these more complicated descriptions still are in accordance with field observations and this constitutes a kind of verification of the model.

The analysis is taken one step further, when an importance value is attached to the various parameters, related to their effect on the population growth rate. Sensitivity analysis, developed initially by Caswell is very useful in this respect. It allows a quick appreciation of a data set and opens the possibility of focussing data collection in the most critical parts of a life history. A much finer picture can now be drawn. First year's survival is most important in both populations but more so in the wet site, seed production is more important in the dry site. The formation of side rosettes is not so much a mode of (vegetative) reproduction, as a method to increase the current year's seed production. It is important in the dry site, but only in the year of formation. Timing of germination has a great impact but seedbank has not. Predation is important especially in the ungrazed situation. Size effects are more pronounced in the wet site, as it should, than in the dry site. All such comparisons are possible only when a model is used.

The ultimate step in the use of the model is the use of population growth rate as a fitness measure and substituting importance value by selective pressure. The line of reasoning runs as follows: When a trait is important for the fitness of a population, it will be under great selective pressure, resulting in low levels of additive genetic variance. Lewontin (1965) for instance predicted low genetic variability in age at first of reproduction in colonizing

species on the basis of his model. Along same lines, the following predictions can be made for the two populations under study: Seed production standardized by size (reproductive effort) should show less additive genetic variability in the population from the dry site than from the wet site. The same can be said for the formation of side rosettes, survival of seeds in the soil and the number of leaves and scapes to minimize the loss through grazing. Size characteristics like length and width of leaves, length of scapes, size of a seed and relative growth rates are more important and therefore less variable in the wet site. Some of these predictions will be evaluated elsewhere (Van Groenendael, 1985c).

Regardless of the functioning of this model, caution is called for when far ranging evolutionary predictions are based on a simple deterministic model, that lacks diploid genetics (and therefore the possibility of selection), density feed-backs and spatial and/or temporal variability, random or otherwise. Much theoretical effort is put into improving the basic model (Smouse & Weiss, 1975; Tuljapurkar & Orzack, 1980; Tuljapurkar, 1982; Caswell, 1983) but a data set to match these complex models is very hard to come by, making an empirical test nearly impossible. This leaves deduction as the only logical alternative as a way to test these models, but predictions, from a model, that is not rigidly confined to empirical boundaries, become dependent on the boundaries chosen by the modeller and run the risk of producing unfalsifiable hypotheses. The following considerations could be of some importance:

- The model contains several complex parameters, that is parameters in which several traits are summarized. Especially when there are negative internal correlations the importance of a parameter can be seriously underestimated.
- Matrix projection models work under the Markovian assumption. This condition forbids any historical effects. The present state of the model may depend only on the state directly preceding the present state. Biologically this is unrealistic. There is, for instance, in the matrices a decreasing survival probability for the transition of size category 1 to size category 1 (small plants remaining small) and an increasing one for the transition of size category 5 to size category 5 (big plants remaining big). Both tendencies are distinct historical effects. To what extent this invalidates the results, obtained from the model, is unclear.
- Sensitivity analysis according to Caswell (1978), assesses the effect of small but absolute changes in the model's parameters. Biologically this is not always realistic. One more seed produced is not equivalent with one more ro-

sette surviving, so that an appropriate biological standardization is called for. Apparent contradictions like the importance of germination in the wrong season as in the present case can then be solved.

- There are biological indications that variability in time and space results in asymmetrically distributed life history traits. Examples are fruit masting for variability in time in a trait like seed production and skew size hierarchies as a result of local effects. Such skewness has a clear effect on fitness expressed as time to extinction.

- The variability in a trait could have an even greater impact on the fitness of a population than its mean value as shown by Tuljapurkar (1982) on theoretical grounds, especially in fluctuating environments. The model could be used now to build more rigorous hypotheses about the effects of variability in traits and this would allow some further testing of the consequences of plasticity (Caswell, 1983; Van Groenendael, 1985b).

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APPENDIX 1

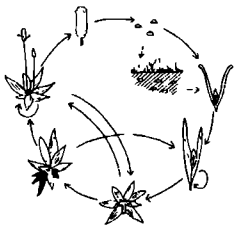
Numerical values of the matrix elements describing the dynamics of a population of *Plantago lanceolata* from a dry dune grassland (see Fig. 1). Values are arranged in 5 x 5 size matrices, except for B and Z elements. These consist of one single row each.

<u>first row</u>					<u>fourth row</u>					<u>ninth row</u>				
B1	0.100	.	.	.	P1a	0.101	.	.	.	P3	0.013	0.095	.	.
B2a	.	.	.	3.094	P1b	0.353	.	.	.		0.013	0.191	0.040	.
B2b	.	.	.	0.314		0.118	0.238	0.520	0.227
B2z	0.206	0.639	1.502	3.960		0.078	0.320	0.682
B3	.	.	0.924	2.706		0.091
B3z	.	.	1.848	3.820	<u>fifth row</u>					<u>tenth row</u>				
B4	.	.	1.848	3.820	P1e	0.101	.	.	.	P3z	0.250	.	.	.
B4z	.	.	2.310	4.785		0.258	0.125	.	.
B5	.	.	2.310	4.785		0.253	0.125	0.194	0.040
B6	.	.	2.310	4.785		0.062	0.521	0.680
<u>second row</u>					<u>sixth row</u>					<u>eleventh row</u>				
B1	0.100	.	.	.	P1z	0.034	.	.	.	P4	0.100	0.167	.	.
B2a	.	.	6.188	.		0.068	0.067	.	.
B2b	.	.	0.627	.		0.120	0.167	0.200	0.050
B2z	0.413	1.277	3.003	7.920		0.145	0.450	0.700
B3	.	1.848	5.412	10.56		0.009	0.100
B3z	.	3.696	7.650	16.67	<u>seventh row</u>					<u>P4z</u>				
B4	.	3.696	7.650	16.67	P2a	0.154	0.107	.	.	P4z	0.100	0.167	.	.
B4z	.	4.620	9.570	16.67		0.077	0.324	0.105	.		.	0.067	.	.
B5	.	4.620	9.570	16.67		.	0.286	0.368	0.167		.	0.167	0.200	0.050
B6	.	4.620	9.570	16.67		.	0.107	0.368	0.750		.	.	0.400	0.650
<u>third row</u>					<u>eighth row</u>					<u>twelfth row</u>				
Z2	.	0.060	0.334	0.625	P2a	0.167	0.097	.	.	P5	0.100	0.167	.	.
Z3	.	0.625	1.650	2.888		0.088	0.323	0.133	.		.	0.067	.	.
Z4	.	0.625	1.650	2.888		.	0.097	0.433	0.333		.	0.167	0.200	0.050
Z5	.	0.625	1.650	2.888		.	0.064	0.333	0.667		.	.	0.400	0.650
Z6	.	0.625	1.650	2.888		0.077
					<u>ninth row</u>					<u>tenth row</u>				
					P2z	0.250
						0.125
						0.125	0.214	0.059
						.	0.571	0.824
						.	0.071	0.118	1.000	

APPENDIX 2

Numerical values of the matrix elements describing the dynamics of a population of *Plantago lanceolata* from a wet hay meadow (see Fig. 2) Values are arranged in 5 x 5 size matrices, except for B elements. These consist of one single row each.

<u>first row</u>		<u>fifth row</u>		<u>twelfth row</u>
B4n	0 240 0 735 3 000	P2a	0 143 0 059	P5a
B4s	0 240 0 735 3 000		0 214 0 235	0 200 0 133
B5a	0 760 2 905 9 440		0 214 0 059 1 000	0 400 0 067 0 100
B5s	0 760 2 905 9 440			0 267 0 367 0 333
B6a	0 760 2 905 9 440			0 133 0 200 0 500
B6s	0 760 2 905 9 440			
B7	0 760 2 905 9 440			
B8	0 760 2 905 9 440	<u>sixth row</u>		<u>thirteenth row</u>
B9	0 760 2 905 9 440	P2s	0 090 0 143	P6a
B10	0 760 2 905 9 440		0 053 0 048 0 286	0 033
B11	0 760 2 905 9 440		0 053 0 095	0 500 0 230 0 151
B12	1 900 4 150 4 130		0 008 0 095 0 286	0 100 0 605 0 684
			0 007	
<u>second row</u>		<u>seventh row</u>		<u>fourteenth row</u>
B4a	0 080 0 242 1 000	P3a	0 181 0 087	P7
B4s	0 080 0 242 1 000		0 181 0 162 0 023	0 333 0 167 0 062
B5a	0 253 0 968 3 147		0 162 0 339	0 333 0 463 0 082
B5s	0 253 0 968 3 147		0 393 0 765 0 457	0 167 0 338 0 748
B6a	0 253 0 968 3 147		0 235 0 544	
B6s	0 253 0 968 3 147	<u>eighth row</u>		
B7	0 253 0 968 3 147	P3s	0 077	
B8	0 253 0 968 3 147		0 300	0 033
B9	0 253 0 968 3 147		0 143 0 333 0 600	0 500 0 230 0 151
B10	0 253 0 968 3 147		0 100 0 400	0 100 0 605 0 684
B11	0 253 0 968 3 147			
B12	0 633 1 383 1 377	<u>ninth row</u>		<u>fifteenth row</u>
		P4a		P8
<u>third row</u>			0 200 0 133	0 033
P1a	0 069		0 400 0 067 0 100	0 500 0 230 0 151
	0 084		0 267 0 567 0 333	0 100 0 605 0 684
	0 005		0 133 0 200 0 500	
	0 005	<u>tenth row</u>		<u>sixteenth row</u>
<u>fourth row</u>		P4s	0 181 0 087	P9
P1s	0 821		0 181 0 162 0 023	0 033
	0 130		0 162 0 339	0 500 0 230 0 151
	0 043		0 393 0 765 0 457	0 100 0 605 0 684
	0 006		0 235 0 544	
		<u>eleventh row</u>		<u>seventeenth row</u>
		P5a		P10
			0 333 0 167 0 062	0 033
			0 333 0 463 0 082	0 500 0 230 0 151
			0 167 0 338 0 748	0 100 0 605 0 684
				<u>eighteenth row</u>
				P11
				0 300 0 091
				0 300 0 546 0 490
				0 182 0 346



THE SIGNIFICANCE OF DIFFERENCES IN
LIFE HISTORIES BETWEEN POPULATIONS OF
PLANTAGO LANCEOLATA L. FROM CONTRASTING
HABITATS USING RECIPROCAL TRANSPLANT
EXPERIMENTS: THE IMPORTANCE OF PLASTICITY

SUMMARY

Two populations of *Plantago lanceolata* from contrasting habitats and with very different life histories have been used in reciprocal transplant experiments to test the significance of the observed differences. Three phases in the life cycle have been tested this way: The survival of seeds buried in the soil, germination and subsequent establishment of seedlings and lastly, survival of adults. The results show strong site effects but also site x origin interaction in the direction of a better performance at the home site. This points at local specialization. After a sufficient period of time for the habitat differences to take full effect, it can be concluded that both populations, summed over their whole life cycle, are unfit to survive in each others habitat. An attempt is made to relate this difference in fitness to specific traits in a number of genotypes from each population. In general there were only weak correlations between any of the traits measured and the individual fitness of the chosen genotypes, except for the number of leaves in a rosette. This is interpreted as supporting the importance of architecture for the fitness of a plantain rosette. For a small number of traits related to the size of a rosette a measure of plasticity could be obtained and related to fitness in the field. The results suggest that plastic responses in size characteristics are an advantage in an unpredictable environment suffering from droughts and low levels of nutrients, whereas such plasticity is a disadvantage in a stable, productive environment, with strong competition for light.

Differences between populations of the same species in different habitats have long attracted the attention of botanists (for reviews see Heslop-Harrison, 1964; Langlet, 1971). One of the reasons for this interest is the successful interpretation of these differences in an evolutionary context, once the genetic basis of such differences has been established. This is why the study of ecotypes has been advocated as a means to unravel the evolution of life history tactics (Stearns, 1976; Etges, 1982; Barbault, 1984) and this view is supported by the results from such studies (Gadgil & Solbrig, 1972; Hickman, 1975; Law et al., 1977; Antonovics & Primack, 1982). As pointed out by Stearns (1977), what is needed are critical tests to show that the genetic differences between ecotypes in life history traits, usually established under laboratory conditions, confer different fitnesses to the ecotypes in the field. Reciprocal transplant experiments between the original habitats have proved to be such a critical test (Turkington & Harper, 1979; Grace & Wetzel, 1981; Lovett-Doust, 1981; Antonovics & Primack, 1982). The interpretation of the transplant experiment in an evolutionary context depends on whether seeds, seedlings raised free from selection or ramets from adults are used (Lovett-Doust, 1981). However, all stages of the life cycle should be tested because of the occurrence of cumulative effects (Hickey & McNelly, 1975), especially in the case of perennial plants. Furthermore, it is important to combine various measures of fitness e.g. size, growth, number of offspring produced or survival. Survival, for instance, might be more important for fitness in unpredictable environments with density-independent regulation, whereas size might prove to be a more important measure in constant environments that are subjected to density-dependent regulation.

In considering the differences in life history traits and their effect on the fitness, it is becoming more and more clear that the variability in such traits could be important as well (Lacey et al., 1983). It has been suggested that the advantage of variability consists in the capacity to track spatial and/or temporal heterogeneity in the environment and that such variability should be plastic rather than genetic when there is unpredictable heterogeneity (Levins, 1968). Mathematically it can be shown that variability in life history traits in unpredictable environments is disadvantageous (Gillespie, 1974; Boyce, 1977; Tuljapurkar, 1982). Caswell (1983) discusses this contradiction and he gives some theoretical examples in which plasticity is advantageous. It remains unclear whether such plasticity should be viewed as comple-

mentary to genetic variation as postulated by Lewontin (1957) or as a protection against selection, thereby maintaining genetic variability as suggested for *Plantago lanceolata* by Kuiper (1984). Plasticity is organized in a trait-specific and environment-specific way and itself under genetic control (Bradshaw, 1965). Although plasticity has frequently been demonstrated, it is termed adaptive rather loosely and used to explain the lack of genetically based local specialization (Hickman, 1975; Warwick & Briggs, 1980; Antonovics & Primack, 1982). A critical test of its effect on fitness, such as a reciprocal transplant experiment has not been performed so far.

In this paper an attempt will be made to test the differences in traits that have been found between two ecotypes of *Plantago lanceolata* for their contribution to fitness in the field, using reciprocal transplant experiments in various stages of the life cycle. The genetic basis of the differences in traits will be explored but with special attention to the plastic variation in these traits. Two ecotypes were selected from habitats that differed in such a way that at least there was some a priori idea where to expect plasticity. One population was growing in an open, nutrient-poor environment suffering from periodic but unpredictable droughts. It was expected to show genetic variability (Istock, 1983) and/or plasticity (Levins, 1968). The other was under strong biotic control growing in a constant and productive environment. It was expected to be genetically more uniform and less plastic (Lewontin, 1965).

MATERIAL AND METHODS

Site description

Plantago lanceolata is a rather short-lived rosette-forming herb, which can grow in a wide variety of (grassland) habitats. It produces long, stalked inflorescences from axillary meristems, which can also produce side rosettes as an alternative. It forms ecotypes quite readily (Böcher, 1943; Primack, 1976; Teramura, 1978), showing substantial genetic differentiation, but it also possesses a high degree of plasticity (Antonovics & Primack, 1982; Kuiper, 1984).

Two populations were selected from strongly contrasting habitats, each of them having been more or less the same for at least a hundred years to ensure continuity in selective forces. The first is an open and dry dune grassland,

which has been grazed as a commonage by cattle and horses for several hundred years (Noë & Blom, 1982). Occasionally and unpredictably, the grassland suffers from catastrophic droughts in spring and summer. The individuals of *Plantago lanceolata* from this site are short-lived. There is a seedbank, juveniles and adults are more or less equally at risk and there is a tendency towards monocarpy. The other site is a permanently waterlogged, closed hay field, situated in a former riverbed, now filled with a thick peat layer. The vegetation is mown once a year in July. The individuals of ribwort Plantain growing here are longer-lived, there is no appreciable seedbank, juveniles carry the great-

Table 1. Characteristic differences between two populations of *Plantago lanceolata* from a dry dune grassland and a wet meadow, respectively.

	dry grassland		wet meadow	
	mean	CV%	mean	CV%
No. of leaves/rosette	6.6	27	3.8	25
Length of longest leaf (mm)	34	24	203	24
No. of ears/genet	9.2	69	1.7	47
Length of scape (mm)	54	61	380	29
Length of ear (mm)	7.3	31	17.1	34
No. of seeds/ear	15.74	75	57.21	53
Seed weight (mg)	0.73	75	1.91	39
No. of side rosettes/rosette	3.6		0	
% adults flowering	31		20	
% rosettes with side rosettes	12		0	
No. of seeds in the soil per m ²	1700		500	
No. of seedlings per m ² 1979	779		1158	
1980	486		465	
% germinating in spring 1979	68		44	
1980	75		46	
% seedlings surviving 1979 → 1980	59		26	
1980 → 1981	45		28	
Half-life adults in months	20		46	
Half-life juveniles in months	18		5	

est risk and the adults are definitely iterocarpic, as they should be according to the postulates of Charnov & Schaffer (1973). The major demographic differences are listed in Table 1 (for full details see Van Groenendael, 1985b).

Three reciprocal transplant experiments were started in the autumn of 1979 and the spring of 1980, testing three phases in the life cycle: Survival of seeds in the soil, germination of seeds and their subsequent survival as seedlings and the growth and survival of young adults.

Reciprocal burial experiments

Seeds collected in the summer of 1979 from both populations and stored dry at 4°C, were buried in each site in nylon mesh tubes, 10 cm long, 2.5 cm diameter and 0.2 mm mesh. The tubes were filled with the soil from the site in which they were to be buried, from which plantain seeds already present were removed by sieving. In each tube ten seeds were placed at 7, at 4 and at 1 cm respectively and the tubes were fitted in holes made with a corer of the same diameter. Before burying, seeds from each origin were divided by hand into five size categories containing approximately the same number. Because of the differences in seed weight between the two origins (see Table 1) the largest size category of the dry site had about the same size as the smallest category of the wet site. Sixteen tubes were prepared for each size category, 160 in all containing 4800 seeds. In each site 80 tubes were randomly placed in a 12 cm grid pattern in the autumn of 1979. Two replicate tubes per size category were retrieved at 4 three-monthly intervals. The tubes were cut into three parts, sieved and the remaining seeds tested for viability in petri dishes placed in an incubator at 22°C. Those seeds that did not germinate within two weeks were cut in two and the embryos tested for viability using tetrazolium staining. The number of surviving seeds was then analysed in a split plot analysis of variance, using the statistical package of GENSTAT (Alvey et al., 1980).

Reciprocal sowing experiment

In the spring of 1980 seeds from the same seed collection, used in the previous experiment, were sown in replicate plots in each site. 400 seeds were placed a few mm deep in a 1 cm grid with fixed corner poles in each plot, in order to be able to discriminate between spontaneous seedlings and seedlings originating from sown seeds. For this purpose two further measures were taken: all seeds

were painted bright red on one side with non-toxic paint. In the laboratory this paint did not affect the level of germination, although there was a few days delay in reaching the maximum level. Similar results were also achieved by Blom & Van Heeswijk (1984) using a different type of paint. Furthermore, two control plots were followed in each site to obtain an estimate of the amount of seedlings that germinate spontaneously. A density of 1 seed per cm^2 is comparable with the seed rain in the field (Van Groenendael, 1985b). Germination was followed over a two year period with gradually longer time intervals. The seedlings that emerged were mapped on transparencies and their survival and size, in terms of number of leaves and length of longest leaf, were recorded. There is a reasonable correlation between above-ground dry weight and number of leaves times the length of longest leaf (Noë & Blom, 1982). The various parameters are analysed by two-way analysis of variance testing the effects of origin, site and their interaction.

Reciprocal transplant experiment

Late in the summer of 1979 10 flowering adults were taken from each site and transferred to the greenhouse where they were allowed to grow freely December. Flowering in the field was taken as a measure of success for that genotype and all genotypes were collected several meters apart to reduce possible local inbreeding effects. In December all adult leaves were cut from the plant at their base and used for vegetative sprouting (Wu & Antonovics, 1976). This way it was possible to obtain a fair number of cloned individuals. In the early spring of 1980, the young plantlets were measured and planted into plastic tubes of 5 cm length and 1.5 cm diameter, half of them containing soil from the dune grassland, the other half soil from the wet meadow. After one week of hardening the plantlets outdoors they were taken to the field, the cores with plantlets taken from the tubes and planted in corresponding holes. Each genotype is represented by 20 individuals, 10 in each site, 200 plantlets per site. The plantlets were planted in a randomized block design, with 1 individual from each origin per block in all possible combinations of genotypes. Survival and size of survivors were recorded at regular intervals over a two-year period, size once again in terms of number of leaves and length of longest leaf. Due to many losses in the dry site, a complete analysis of size in the randomized block design is restricted to the first period of three months after planting. To reduce the effect of size at planting growth over the first

three months was chosen as a variable and analysed by analysis of variance, using the regression technique provided by GENSTAT (Alvey et al., 1980), in order to correct for missing values as a result of death of individuals during the first three months. Survival was analysed using χ^2 -analysis, for the comparison of the survival patterns of the 10 genotypes per origin over the two sites. For a further analysis of survival a different approach was chosen. To estimate survival per origin and per site, 10 random combinations of genotypes were made per origin and per site, resulting in 10 estimates of survival. These were analysed in a two-way analysis of variance.

Three vegetative sprouts per genotype were kept as a control in the greenhouse. Ten traits were measured in each plant to have a characteristic of each genotype for comparison with the same genotypes in the field later on. Analysis of variance provided an estimate of the degree of genetic determination in a trait for each origin by comparing the between-genotype component of variance with the within-genotype component of variance. Per origin all possible correlations between genotypes were calculated based on the mean trait values as well as all correlations between traits based on mean genotype values. Principal components were then extracted from both correlation matrices, using Principal Component Analysis (PCA) from GENSTAT (Alvey et al., 1980). The first two components are used to characterize the genotypes as well as the traits. The results can be plotted in the same diagram, because both are derived from the same data set. This way the relation between traits and genotypes can be demonstrated. After this, Canonical Variate Analysis (CVA) from the same statistical package was applied. This multivariate analysis is based on variance/covariance matrices and offers the opportunity to weight each trait for its within-genotype variability. When this component of variance is high compared with the between genotype component, the effect of a trait is weighted down correspondingly. The first two canonical variates are used to arrange both genotypes and traits in this reduced 'genotypic' space, whereas they were arranged by PCA in a more 'phenotypic' space.

RESULTS

Reciprocal burial experiment

From field samples laid out in the laboratory for germination, it was clear that there were more seeds in the seedbank in the dry site than in the wet site.

Table 2. Split plot analysis of variance for survival of seeds from two populations of *Plantago lanceolata* buried reciprocally in their own and the other habitat. Missing values are substituted by estimated values calculated according to GENSTAT (Alvey et al., 1980).

	DF	F	P
Replication x plot stratum			
Replication	1	0.017	ns
Time	3	108.715	< 0.001
Site	1	3.501	< 0.1
Origin	1	0.744	ns
Size	4	11.953	< 0.001
Time x site	3	4.176	< 0.01
Time x origin	3	2.827	< 0.05
Site x origin	1	1.047	ns
Time x size	12	0.655	ns
Site x size	4	2.060	< 0.1
Origin x size	4	12.990	< 0.001
Time x site x origin	12	2.221	< 0.025
Time x site x size	12	0.734	ns
Time x origin x size	3	0.239	ns
Site x origin x size	4	2.899	< 0.05
Residual	84(7)		
Replication x plot x depth of stratum			
Depth	2	85.860	< 0.001
Depth x time	6	2.883	< 0.01
Depth x site	2	5.989	< 0.005
Depth x origin	2	6.378	< 0.005
Depth x size	8	2.194	< 0.05
Depth x time x site	6	3.244	< 0.005
Depth x time x origin	6	1.254	ns
Depth x site x origin	2	4.004	< 0.025
Depth x time x size	24	0.972	ns
Depth x site x size	8	0.755	ns
Depth x origin x size	8	0.584	ns
Residual	232(14)		

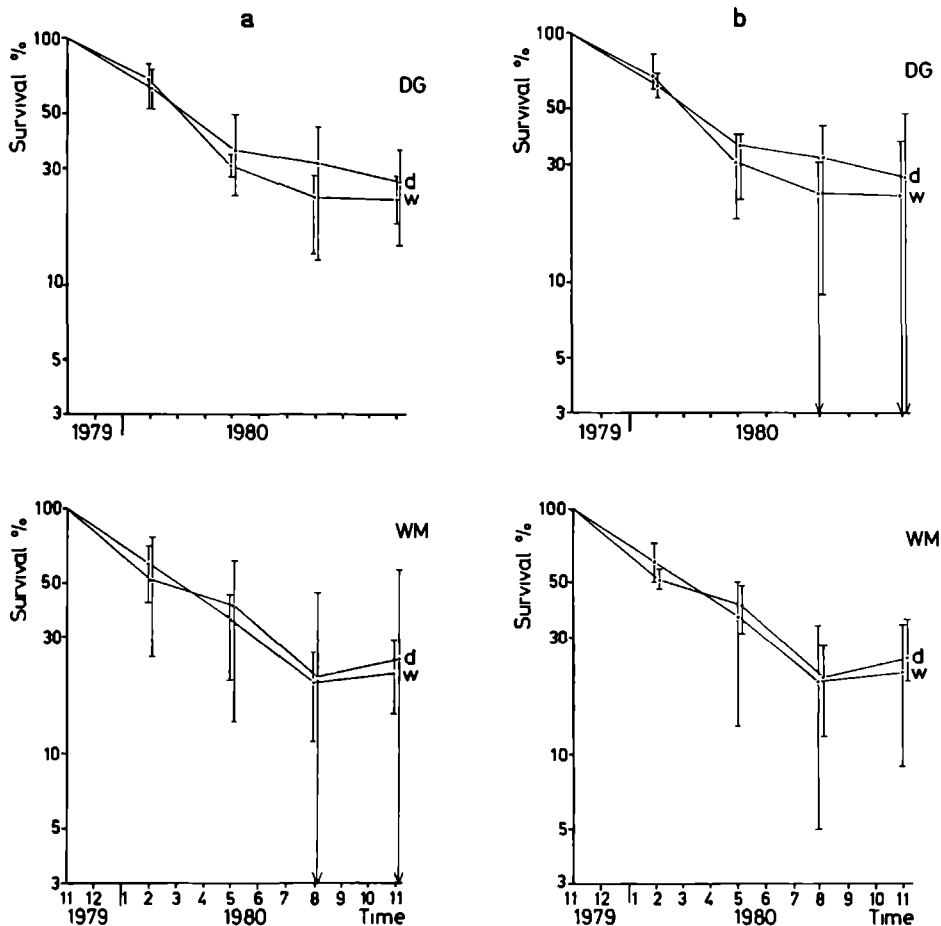


Figure 1. Survivorship curves of two cohorts of seeds of *Plantago lanceolata* buried reciprocally into a dry grassland (DG) and a wet meadow (WM), respectively. Origin of the seeds is indicated by d (dry grassland) and w (wet meadow). Bars indicate the range between smallest (lower end) and biggest (upper end) seeds (a) or the range between burial near the surface at 1 cm (lower end) and burial at 7 cm (upper end) (b).

The question is whether the dry site is more favourable for survival of seeds in the soil or whether the seeds of different origins possess different properties, like a stronger dormancy as shown for seeds from the dry site in labora-

tory germination tests (Van Groenendael, 1985b).

When each population survives best in its own habitat, this indicates local specialization, observable as a site x origin interaction in the analysis. When inspecting the results of the split-plot analysis of variance (Table 2), the survival of seeds in the soil is mainly determined by burial time, depth of burial and seed size, with the best survival for big seeds, buried deep (Fig. 1a+b). Because size was relative within each population, the great differences in absolute seed weight (see Table 1) show up as strong origin x size interaction. The smallest seeds in the absolute sense are the smallest seeds from the dry population. These seeds show a lower survival than the smallest seeds from the wet population, which happen to be as big as the biggest seeds from the dry site. Seed decay is faster in the wet site (time x site interaction) and faster for seeds buried near the surface, probably because of germination of these seeds from the surface layer (depth x time interaction). Therefore mean survival is better for seeds buried deep in the dry site (depth x site interaction) and for those originating from the dry population (depth x origin interaction).

There is no significant site x origin interaction indicating local specialization, but local specialization becomes apparent after taking into account the size of the seeds (site x origin x size interaction) and can be attributed mainly to small seeds of the dry population doing relatively badly in the alien habitat (see Fig. 1a). Local specialization is also found after correcting for depth of burial (site x origin x depth interaction), because of the relatively higher survival of seeds from the dry population buried near the surface in their own habitat (see Fig. 1b).

The overall picture is that there are indications for local adaptation for survival of seeds in the soil. This is best expressed in the dry site, where there is no extra risk for the smaller seeds produced in this habitat, whereas such small seeds are easily lost in the wet meadow. Seeds from the dry site also survive better in the surface layer of the soil. Moreover, as far as survival of seed is concerned, it is not a great disadvantage to have small and very variable (Table 1) seeds in the dry site. The significance of this is illustrated by the fact that seeds are produced in the dry site under unfavourable conditions, in which not all seeds can be filled appropriately. There is a significant negative correlation between the number of seeds per mm of ear and the mean weight of seeds in that ear, whereas there is no such correlation in the population from the wet site (Van Groenendael, 1985b). The results of this reciprocal burial experiment are consistent with the observed differences in seedbank in both populations (Table 1).

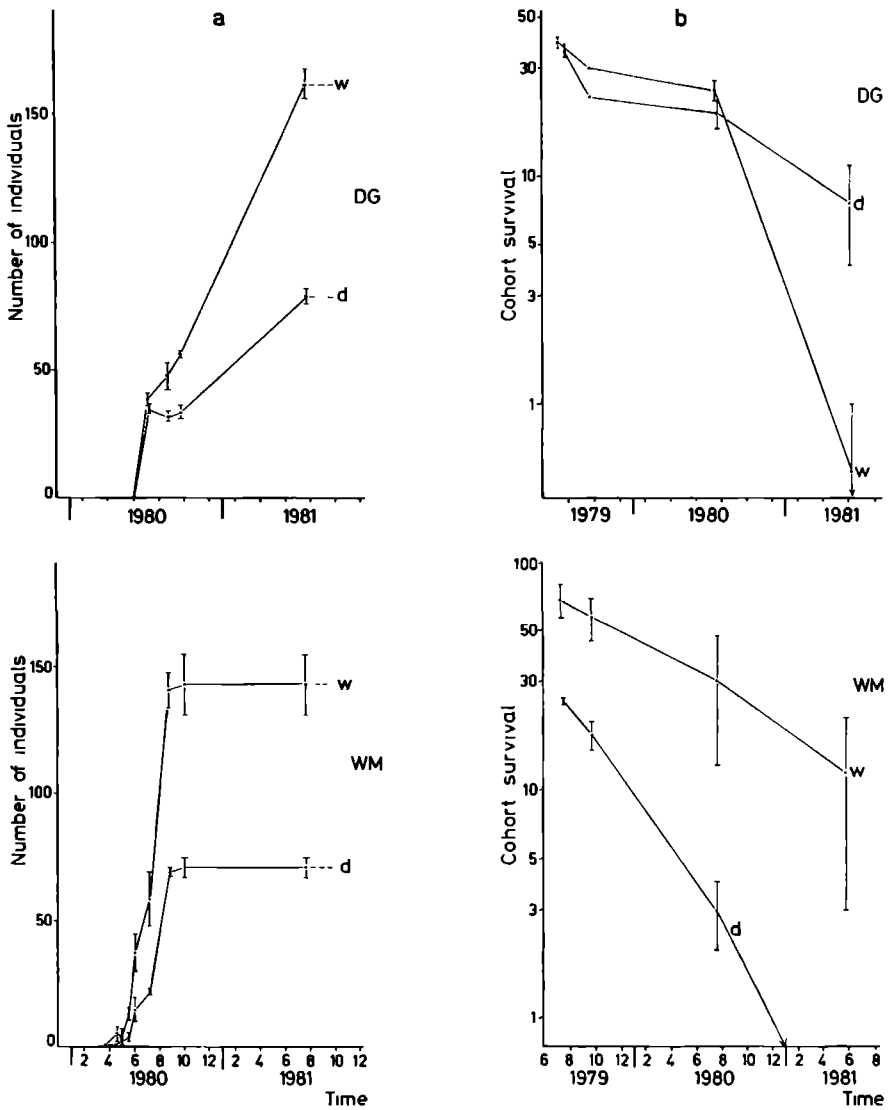


Figure 2. Germination characteristics for two populations of *Plantago lanceolata* sown reciprocally into a dry grassland (DG) and a wet meadow (WM), respectively. Origin of the seeds is indicated by d (dry grassland) and w (wet meadow). Bars indicate the range between two replicate plots (a). Survivorship curves for the spring cohorts of seedlings from the reciprocal sowing experiment are presented as well (b).

Table 3. Two-way analysis of variance for various traits of two populations of *Plantago lanceolata* sown in their own and the other habitat, respectively. 1 based on two replicate plots per site and per origin (DF error = 4). 2 based on 30 seedlings selected at random per site and per origin (DF error = 116). 3 based on 20 seedlings selected at random per site and per origin (DF error = 76).

	Total number of germinated seeds (1)		Survival after 1 yr spring cohort 1979 (1)	
	F	P	F	P
Origin	204.38	< 0.001	4.55	< 0.1
Site	19.23	< 0.05	15.67	< 0.05
Origin x site	0.37	ns	0.44	ns

	Survival after 2 yrs spring cohort 1979 (1)		Survival 1st to 2nd yr spring cohort 1979 (1)	
	F	P	F	P
Origin	0.10	ns	0.83	ns
Site	0.10	ns	0.05	ns
Origin x site	5.61	< 0.10	11.90	< 0.05

	Length of cotyledon spring cohort 1979 (2)		Length of longest leaf spring cohort 1979 (2)	
	F	P	F	P
Origin	12.21	< 0.001	54.44	< 0.001
Site	76.90	< 0.001	82.97	< 0.001
Origin x site	3.23	< 0.1	15.36	< 0.001

	Growth between 27-7 and 29-9-1979 (3)		Size at 29-9-1979 (3)	
	F	P	F	P
Origin	7.02	< 0.01	25.09	< 0.001
Site	20.37	< 0.001	4.10	< 0.05
Origin x site	0.36	ns	1.40	ns

The reciprocal sowing experiment covers two aspects: the germination response (Fig. 2a) and subsequent survival of seedlings (Fig. 2b).

From the survival of seeds in the soil some dormancy was expected for seeds from the dry population and this is confirmed by the germination pattern (Fig. 2a, Table 3). There is a strong effect of origin on the level of germination. In the dry site seeds from both sources germinate slightly better in the end. Although not tested, the shape of the germination curves shows a remarkable resemblance between origins per site. The somewhat retarded start for seeds from the dry population in the cooler wet meadow can be explained from a higher temperature requirement for germination for seeds in this population (Van Groenendael, 1985b).

Survival of seedlings is a much more complex process and the result may be judged only after all relevant risks have been mastered. In this experiment significant site x origin interaction is achieved only after the first periodic drought in the dry dune grassland, which happened to be in the spring of the third year. Local adaptation expressed as a better relative survival in the own habitat becomes apparent then, with virtually no members of the alien population surviving (Fig. 2b; Table 3).

Several properties of the young seedling might be of interest in its struggle for survival, e.g. the length of its linear cotyledon, when it is trying to catch some light penetrating through the canopy (Mook et al., 1981). Cotyledons are longest in the wet site for both populations as a result of etiolation in the dense vegetation. They are also longer for the wet population irrespective of site, because of the larger seeds and the correlation between seed size and cotyledon length ($r = 0.6920$; $n = 40$; $p < 0.01$ for the wet population and $r = 0.6948$; $n = 50$; $p < 0.01$ for the dry population under laboratory conditions). Again irrespective of site, the wet population pushes up a longer leaf. In the wet site this elongation is enhanced for both origins but much stronger so for seedlings from the own habitat, resulting in a strong interaction term. Growth rate, based on estimated above ground biomass, is reduced in the wet site under light-limited conditions, but whether in shade or in full daylight, seedlings from the wet population grow faster. This higher growth rate, together with early germination (see previous section), bigger seeds, longer cotyledons and first leaf, produces larger plants at the end of the first season for the wet population. These larger plants have a better chance

for survival under competitive conditions, but this larger size could be a disadvantage in the dry site. This seems likely, given the survival pattern after the first period of drought in the third year.

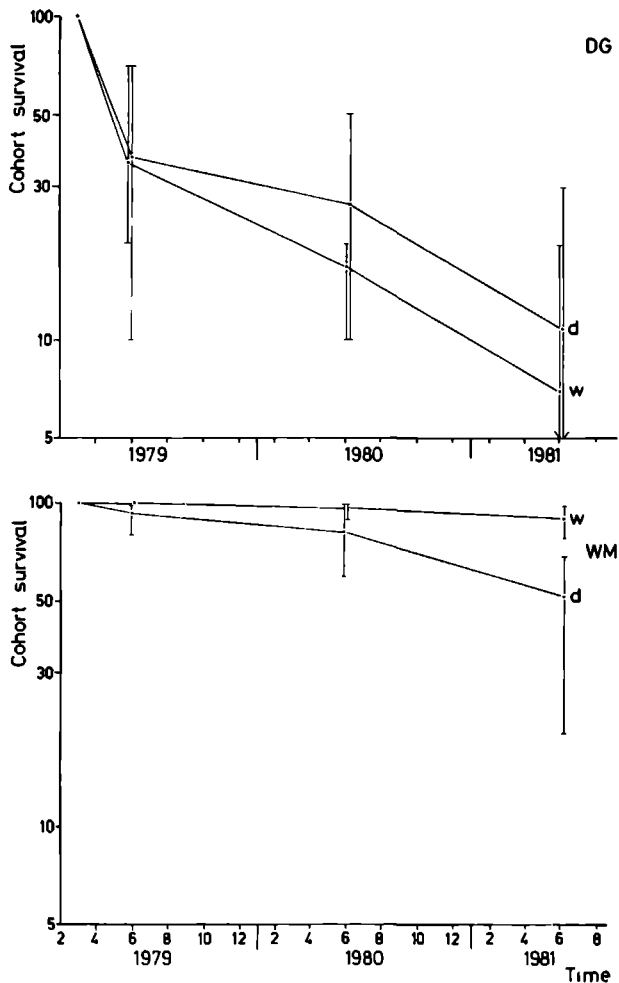


Figure 3. Survivorship curves for juvenile transplants of *Plantago lanceolata* originating from a dry grassland (d) or from a wet meadow (w) and transplanted into both habitats labelled DG (dry grassland) and WM (wet meadow) respectively. Bars indicate the range between the best and the worst surviving genotype.

Reciprocal transplant experiment

As in the previous experiment, survival of adults is best in the wet site and each population is surviving best in its own site (Fig. 3). In the beginning the site effect is strong, but gradually the effect of origin develops, resulting in a better survival in the own habitat (Table 4). This contrast is strong-

Table 4 Two-way analysis of variance for survival of young adults of two populations of *Plantago lanceolata* transplanted reciprocally in their own and the other habitat. χ^2 -values for the comparison of survival pattern for the ten genotypes per population between both sites are presented as well.

	DF	Survival after 3 months		Survival after 1 year		Survival after 2 years	
		F	P	F	P	F	P
Origin	1	0.47	ns	1.06	ns	29.3	< 0.001
Site	1	248	< 0.001	483	< 0.001	399	< 0.001
Origin x site	1	0.47	ns	11.65	< 0.01	42.5	< 0.001
Residual	36						
χ^2 dry population	9	17.75	< 0.05	14.05	ns	16.71	< 0.1
χ^2 wet population	9	0.01	ns	9.64	ns	11.33	ns

est for the wet population, with little variation in survival between genotypes, whereas the contrast is less extreme for the dry population, where there is also more differentiation between genotypes. The genotypes from this population with an above-average survival in their own habitat have a below-average survival in the alien habitat and vice versa, as indicated by the χ^2 -values (Table 4).

Due to the many losses in the dry site an analysis of size characteristics is restricted to the first census, three months after planting. The difference in growth between all possible pairs of genotypes from both habitats is calculated in both sites and used in an analysis of variance (Table 5). The differ-

Table 5. Analysis of variance for the differences in growth over the first three months between pairs of genotypes from two populations of *Plantago lanceolata* originating from a dry grassland (d) or from a wet meadow (w) and transplanted reciprocally in a randomized block design into their own and the other habitat. Growth is based on estimated biomass (m).

	$\ln(m_2/m_1)_d - \ln(m_2/m_1)_w$		
	DF	F	P
Site	1	5.03	< 0.05
Origin d	9	0.92	ns
Origin w	9	1.35	ns
Origin d x site	4	3.87	< 0.01
Origin w x site	6	2.03	ns
Origin d x origin w	48	0.90	ns
Residual	30		

ence was significantly affected by site, being largest in the wet site due to lesser growth for the dry genotypes. In the dry site growth was strongly but equally reduced for both origins as a result of a spring drought. The difference between the two populations is accentuated by the site x origin interaction, which is significant for the dry population.

DISCUSSION

Comparison between field and greenhouse

The measurements in the greenhouse on the same genotypes that were used for the adult transplant experiment show that traits in genotypes from the dry site are generally more plastic than the same traits in genotypes from the wet site (Table 6). The F-values for the between-/within-genotype comparison of components of variance are a measure for the way a trait is expressed in clonally propagated offspring. When high the plants from one genotype resemble each other closely with respect to that trait and differ from all other genotypes. These F-values are somewhat lower and the variability, calculated as the coef-

Table 6. Means and coefficients of variation for several morphological traits of two populations of *Plantago lanceolata* measured in clonally propagated offspring from 10 genotypes from each origin grown in the greenhouse. F-values for the comparison of between- and within-genotype variability are presented as well.

	dry grassland				wet meadow			
	mean	CV%	F 9/20	P	mean	CV%	F 9/20	P
No. of leaves	12.93	31	2.87	< 0.05	15.03	18	2.06	< 0.1
Length of leaf (cm)	12.47	28	4.55	< 0.01	20.07	23	11.30	< 0.001
Width of leaf (mm)	13.83	42	2.82	< 0.05	20.57	32	4.49	< 0.01
Estimated biomass	242	82	2.07	< 0.1	647	50	4.26	< 0.01
No. of ears	28.3	44	1.76	ns	6.3	63	11.50	< 0.001
Moment of flowering	1.33	63	2.70	< 0.05	2.87	65	5.29	< 0.001
Length of scape (cm)	39.2	20	6.88	< 0.001	53.20	16	4.46	< 0.01
Length of ear (mm)	28.0	25	9.07	< 0.001	39.83	32	6.46	< 0.001
No. of seeds/ear	52.9	40	12.15	< 0.001	92.3	36	1.45	ns
No. of side rosettes	9.20	48	5.86	< 0.001	1.87	118	3.82	< 0.01

ficient of variation, usually somewhat higher in the population from the dry site (Table 6). As far as coefficients of variation are compared, this is done under the assumption that there is a linear relationship between mean and standard deviation. Biologically, this seems a reasonable assumption. This is supported by significant positive correlations between mean and standard deviation of nine morphological traits in Table 6 calculated for the ten genotypes within each origin (11 out of 18 correlations were significant). The performance of the genotypes from the wet site seems genetically more fixed. This could explain the better overall survival of the genotypes from the dry site in the adult transplant experiment (Fig. 3). Note that there is a striking contrast in components of seed yield between the two origins, e.g. number of ears (highest F-value in the wet and lowest in the dry population) and number of seeds per ear (vice versa). As far as the F-value represents an estimate of the heritability, albeit an overestimate, it seems that there has been strong selection for the number of ears in the dry site but not so much on the number of seeds per ear. The reverse is found in the wet site. Ecologically, this makes sense, given the long history of grazing in the dry site and the difficulty in producing many inflorescences in the wet site, so that each ear should be as long as possible.

Table 7. Means and coefficients of variation for four morphological traits of two populations of *Plantago lanceolata* measured in clonally propagated offspring from ten genotypes originating from a dry grassland or from a wet meadow transplanted reciprocally into their own and the other habitat. F-values for the comparison of between- and within-genotype variability are presented, whenever their calculation was possible.

	wet site after one year							
	dry grassland				wet meadow			
	mean	CV%	F 9/90	P	mean	CV%	F 9/90	P
No. of leaves	2.74	33	2.14	< 0.05	3.57	29	2.40	< 0.05
Length of leaf (cm)	8.56	43	1.06	ns	13.40	25	1.89	< 0.1
Width of leaf (mm)	5.69	58	1.43	ns	10.96	40	2.44	< 0.05
Estimated biomass	19.1	133	1.37	ns	60.8	67	2.41	< 0.05

	dry site after one year							
	dry grassland				wet meadow			
	mean	CV%	F	P	mean	CV%	F	P
No. of leaves	3.63	42	-	-	4.59	48	-	-
Length of leaf (cm)	2.78	36	-	-	3.33	33	-	-
Width of leaf (mm)	3.78	54	-	-	6.88	62	-	-
Estimated biomass	5.1	126	-	-	18.7	119	-	-

Four of the traits measured in the greenhouse could also be obtained from plants in the field. In the wet site there were enough survivors to calculate a F-value for the comparison between between-genotype and within-genotype components of variance. Although the significance levels are reduced, they confirm the contrast between the dry and wet population in traits measured in the greenhouse (Table 7).

The next step is to define the fitness of the various genotypes in the field and to try and associate a trait or a combination of traits measured in the greenhouse with this measure of fitness, thus establishing its adaptive significance. Fitness of various genotypes in this context is defined in two ways. The first is the sum of all biomass produced by a genotype in a site, summed over the three census dates. It combines in fact growth and survival. The second is the sur-

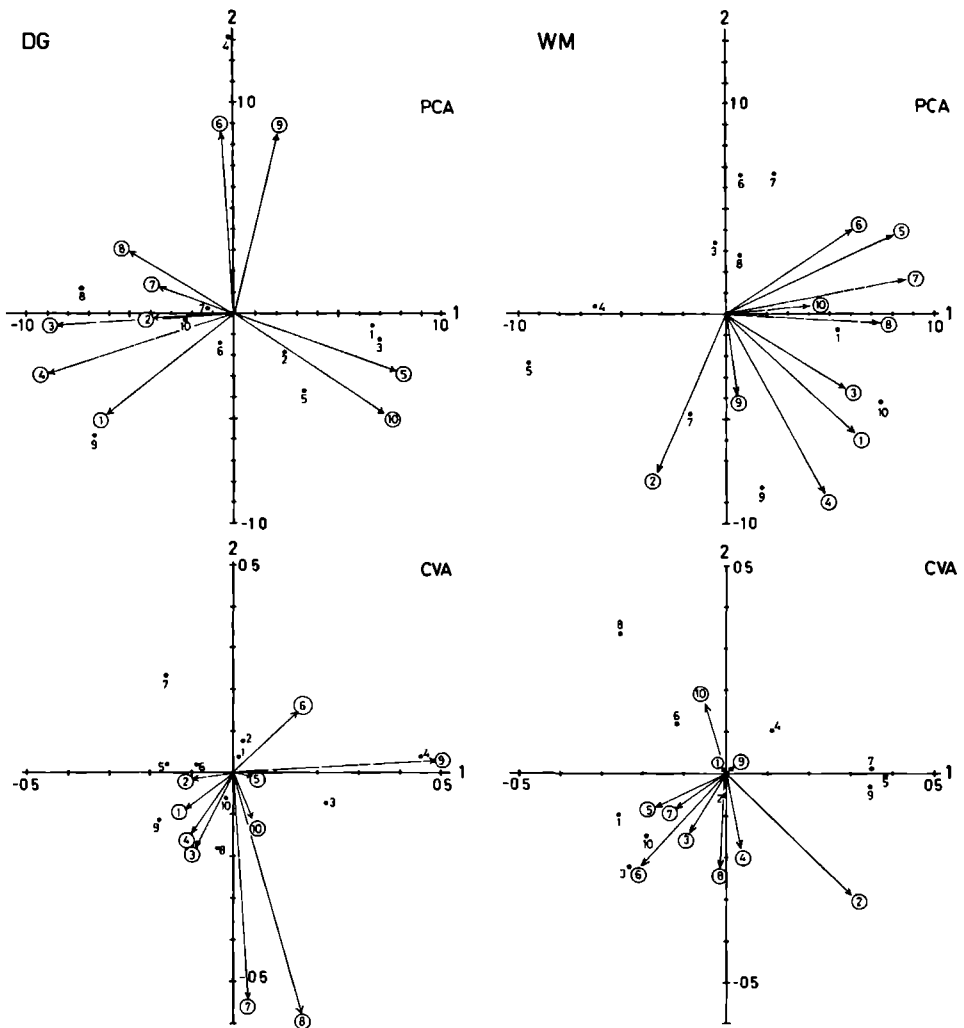


Figure 4. Multivariate characterization of genotypes (dots) by traits and of traits (arrows) by genotypes. Ten genotypes, originating from a dry grassland (DG) or from a wet meadow (WM) were raised in the greenhouse and characterized by ten traits i.e. number of leaves (1); length of longest leaf (2); width of longest leaf (3); estimated biomass (4); number of ears (5); moment of flowering (6); length of longest scape (7); length of longest ear (8); number of seeds per ear (9) and number of side rosettes (10). Principal component analysis (PCA) stresses the phenotypic relations and canonical variate analysis (CVA) stresses the genotypic relations (see text).

vival in each site after two years. These fitness values are then compared with various traits measured in the greenhouse. The measurements in the greenhouse are summarized in two multivariate analyses (Fig. 4). The advantage of this procedure is that the genotypes are defined on the basis of all traits measured and given single values on the axes of PCA or CVA. The relation between a genotype and a trait follows directly from the projection of the genotype vector onto the various trait vectors. The picture, however, simplifies the variability present. Of the total variance 58% and 59% are accounted for in the first two axes of the PCA for the wet and the dry population, respectively. For the CVA this is 80% and 72%, respectively. The values of the genotypes on the first axes in both multivariate analyses are now correlated with the fitness measures defined above (Table 8).

Table 8. Matrix of correlation coefficients between fitness measures in a reciprocal transplant experiment in the field (1 - 4), performance in the greenhouse (5 - 6) and two measures of plasticity (7 - 8, see also Table 9) for ten genotypes originating from two populations of *Plantago lanceolata* (n = 10; significance levels are 0.549, 0.632 and 0.765 for $p < 0.1$, $p < 0.05$ and $p < 0.01$, respectively).

	1	2	3	4	5	6	7	8
wet meadow								
1 Biomass home	-	0.290	0.443	-0.129	-0.034	0.045	-0.836	-0.154
2 Biomass away	-0.132	-	0.005	0.189	0.534	0.283	-0.342	0.308
3 Survival home	0.605	-0.143	-	-0.364	-0.732	0.431	-0.588	-0.657
4 Survival away	0.306	0.564	-0.067	-	0.388	-0.076	0.156	0.165
5 First axis of PCA	-0.551	0.164	-0.102	-0.271	-	-0.611	0.178	0.666
6 First axis of CVA	-0.174	0.666	-0.483	0.487	0.373	-	0.077	-0.766
7 CV of means (CV_1)	0.163	-0.572	0.056	-0.058	-0.591	-0.743	-	0.158
8 Mean CV (CV_2)	0.446	-0.144	-0.020	0.150	-0.853	-0.309	0.571	-
dry grassland								

In the dry population there is a significant positive correlation between the first axis of the CVA and the biomass produced in the alien habitat. Genotypes 4 and 3 do best in the wet meadow and relatively poorly in their own

habitat, given the negative correlations between survival at home and the first axis of the CVA. Types 7 and 9 produce little biomass in the wet meadow, but genotype 9 is the best in his own site. Clearly the traits measured in the greenhouse, when taken together, have some bearing on the fitness of the dry genotypes in the field. It is not clear, however, why genotype 4 for instance that produces many seeds per ear and flowers late in the season, as indicated by trait vectors 6 and 9, should be particularly successful in the hay meadow. The critical trait for fitness is apparently not measured, but it should have some relation with this aspect of seed production. An association with a large number of leaves, as is the case for genotype 9, is more understandable, as a large number of leaves forms the basis for the formation of side rosettes and the many inflorescences, typical for the dry population (Van Groenendael, 1985a).

In the wet population there is a significant negative correlation between survival in the home site and the first axis of the PCA. The relationship is reversed for biomass produced in the alien site, although not significantly, indicating some degree of specialization in the genotypes. Genotypes 5 and 4 survive best in their own and worst in the alien (dry) site, and they seem to be negatively correlated with traits such as number of ears and number of side rosettes, associated with the dry population. Genotype 1 is positively associated with these traits and is together with genotype 10, most successful in the dry site. Genotype 10 is characterized by many leaves, which is advantageous in the dry site as explained above.

The importance of plasticity

As the various genotypes, used in the adult transplant experiment, are represented by a number of individuals in each of three habitats, the greenhouse, the wet and the dry site, plasticity can be expressed in two ways. The first is the coefficient of variation of a trait within one genotype between habitat mean values. The second is a within-habitat coefficient of variation, calculated as a mean of the three coefficients of variation in each habitat. The coefficient of variation associated with this mean is an indication how different the variability is in a trait in various habitats and expected to be low when there are comparable plastic responses in the three habitats (Table 9).

These two measures of plasticity need not be the same. If plasticity is defined as the capacity to produce various phenotypes from one genotype, with

Table 9. Population mean values of various coefficients of variation for four traits, calculated over 10 genotypes of *Plantago lanceolata*, originating from two contrasting habitats. CV_1 coefficient of variation calculated over three mean trait values in three habitats: Greenhouse, home site and alien site. CV_2 mean coefficient of variation averaged over the three within-habitat coefficients of variation. CV_3 coefficient of variation in CV_2 . Per genotype each coefficient of variation is averaged over the four traits and the population mean values of these averages is presented as total mean. The correlation coefficient between CV_1 and CV_2 is presented as well (r). For levels of significance see Table 8.

	dry grassland				wet meadow			
	CV_1	CV_2	CV_3	r	CV_1	CV_2	CV_3	r
Number of leaves	71	28	49	0.286	86	25	68	-0.594
Length of longest leaf	61	25	52	-0.359	68	23	62	0.417
Width of longest leaf	66	34	55	0.381	72	33	66	0.023
Estimated biomass	116	61	51	0.652	135	59	62	0.308
Total mean	65	37	52	0.571	75	35	65	0.158

a genetically controlled range of possibilities, then a greater range, expressed as within-habitat variability could reduce the between-habitat variation, so that both proposed measures will be antagonistic instead of expressing the same capacity to produce different phenotypes under different conditions. Four traits could be measured for all genotypes in all habitats to test this hypothesis, using the first census for the field data, in order to have as many individuals as possible. There is no consistent positive nor negative correlation between within- and between-habitat variability in either population. Both measures represent different and apparently unrelated aspects of plasticity (Table 9). However, the fact that the within-habitat component (CV_2) is constantly larger in the dry population and the between-habitat component (CV_1) constantly smaller than in the wet population indicates a trade-off confirming the hypothesis. This is also supported by the fact that the within-habitat component is more constant over the three habitats in the dry population (CV_3), which could indicate that the greater extremes between habitats are buffered away.

Genotypes which are in general more plastic in the four morphological traits used above have a reduced fitness in the wet meadow, irrespective of origin. This is expressed by negative correlations between plasticity of genotypes,

expressed as the coefficient of variation between habitat mean values (CV_1) and the biomass produced in the wet meadow (Table 8). This disadvantage of plasticity is most apparent for the local genotypes. Those genotypes that possess the highest degree of plasticity, whether from the dry site or from the wet site, are also associated with a position in the multivariate analyses, where those genotypes are located which do well in the dry dune grassland and not in the wet meadow. Those genotypes which possess the lowest degree of plasticity, again irrespective of origin, do well in the wet meadow and are associated with the opposite positions in the multivariate analysis (Table 8). All this confirms the frequently stated belief that plasticity enhances fitness in unpredictable environments. Such plasticity, which can be advantageous in one and disadvantageous in another habitat in the same set of traits, demonstrates that the relation between plasticity and fitness cannot be defined outside a specific environment. Adult size characteristics are probably directly influencing the fitness of an individual in a competitive environment. Under these conditions plasticity is a disadvantage. On the other hand a big size could be a disadvantage in the dry site, negatively influencing fitness. Variability in size might be the answer for individuals to adapt and survive the variable conditions. Under such conditions plasticity could be an advantage.

CONCLUSIONS

The two populations of *Plantago lanceolata*, used in this study, show rather contrasting life histories. The differences between the two populations have a clear genetic basis. This is true for an array of morphological characteristics, but also for demographic traits like germination and survival. These differences result in local specialization when tested in reciprocal transplant experiments. Buried seeds survive better in their own habitat. This is most apparent in the population from the dry site. The small and variable seeds from this site do not survive very well in the wet marshy soil. Survival in their own habitat is better, partly because they keep better and partly because dormancy prevents an easy germination. This dormancy also influences the germination response, being lower for the dry population, but equally so in both habitats. Survival of seedlings and of juveniles again shows local adaptation. Each population survives best in its own habitat. In this phase of the life cycle the contrasts are most pronounced for the wet population. The reason is that this

population has longer cotyledons and a longer first leaf, which results, in combination with a higher relative growth rate, in a sufficient competitive ability under light-limiting conditions. In the dry dunes these plants grow to such a large size that they cannot withstand any prolonged period of drought, which causes them all to die.

When considering the results of the three reciprocal transplant experiments, it seems very unlikely that populations could establish themselves in the wrong habitat. This conclusion would not have been equally clear if only one phase had been tested and this stresses the importance of studying the entire life cycle. Another important point is that monitoring of the experiments should continue until all hazards of life have occurred, because only then has full reciprocity been achieved. The strength of the reciprocal transplant experiments is their capacity to demonstrate unambiguously local specialization. Several traits could be identified which are responsible for this specialization e.g. seed size, dormancy, length of cotyledon and first leaf, growth rate and adult size. However, the notion of local specialization on the level of a population, based on differences in traits, only makes sense if one can demonstrate at the same time differences in fitness for the individual, based on the same traits. Differences in fitness between individuals of each population could in general be associated with differences in a set of adult size characteristics in a global way, using multivariate analysis. The number of leaves was the only trait that could be identified as a single important fitness character and this makes sense, given the crucial role of this character in the architecture and the allocation pattern of the plantain rosette. A more general characteristic in adult size characteristics, which proved to be associated with differences in fitness, was plasticity, here defined as the within-genotype variability, both within and between habitats. Plasticity, as a trait in a trait, was more important in the dry than in the wet population, and it was also more constantly expressed between habitats in the dry population. However, irrespective of origin, plasticity was advantageous in the dry and disadvantageous in the wet site. This supports the idea that plasticity is important in unpredictable environments.

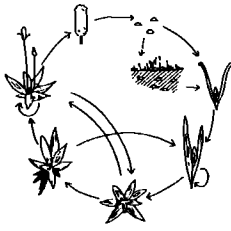
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DIFFERENCES IN LIFE HISTORIES BETWEEN TWO
ECOTYPES OF *PLANTAGO LANCEOLATA* L.:
THE POSSIBLE IMPORTANCE OF ARCHITECTURE

SUMMARY

Plantago lanceolata L. is a short lived herb from grassland habitats and reported to form ecotypes quite easily. Two populations were selected from contrasting habitats: a dry, grazed dune grassland and a permanently waterlogged hay meadow. Their contrasting life histories have been recorded with standard demographic techniques. Matrix projection models have been used to predict the long term implications of both life histories and to assess the sensitivity of the population growth rate for (small) changes in life history parameters. Using Fisher's theorem, these sensitivities can be used to predict selection pressures and therefore low additive genetic variances in the most sensitive parameters.

The models predictions are compared with the results of three reciprocal transplant experiments in different phases of the life cycle and with a laboratory test, involving cloned individuals from both habitats. Transplant experiments showed differences in fitness as a result of the differences in life history parameters and the laboratory test revealed differences in genetic control in a selected set of traits. Both tests confirmed the predictions of the sensitivity analysis.

Finally, the concept of a life history strategy as a set of co-adapted traits, is discussed. Somehow a more general principle open to selection must underly such a set of life history traits. The control over meristematic activity during plant morphogenesis is proposed as a more general regulator.

It has been argued by Harper (1982) that taxonomic categories fail as descriptors of ecological entities because of the bias in taxonomy towards stable, conservative characters that can be used to define a taxon. Those characters that enable a plant to survive in a specific habitat and that are of interest to an ecologist are varying as a reaction to the variable conditions in which that plant grows. Such a variability could be the result of plasticity of the individual as well as of genetic differences between the individuals. Habitat related genetic differences between populations have been an object of study for a long period of time (Heslop-Harrison, 1964; Langlet, 1971). All sorts of characters in plants, including life history traits, have been reported to show ecotypic variation; in general, these have resulted from strong and readily identifiable selective forces (Turesson, 1925; Antonovics, Bradshaw & Turner, 1971; Gadgil & Solbrig, 1972; Law, Bradshaw & Putwain, 1977; Warwick, 1980).

Usually, the genetic variation between ecotypes is established by growing them under uniform conditions in the greenhouse or experimental garden and testing them in experiments with the selective force as a variable. When dealing with complex life history traits like survival or fecundity, it can be especially difficult to estimate the genetic variation (Lewontin, 1974; Primack & Antonovics, 1981). Furthermore, in an evolutionary context it is not sufficient to establish the presence of genetic variation, it is also necessary to demonstrate fitness differences as a result of the genetic differences in the traits under consideration. A powerful test in this respect, especially when working with ecotypes, consists of reciprocal transplanting and measuring the actual fitness differences (Antonovics & Primack, 1982). An indirect test is based on the assumption that strong selection on important traits must result in relatively low levels of additive genetic variance (Lewontin, 1965; Stearns, 1977; Schmidt & Lawlor, 1983).

An important tool when dealing with life history traits, is the sensitivity analysis developed by Caswell (1978). This analysis is applied in matrix projection models describing the growth of a population and was originally developed by Lewis (1942) and Leslie (1945). It calculates the sensitivity of the population growth rate λ to small changes in the model parameters. Since this population growth rate can be used as a measure of the fitness of a population (Fisher, 1958; Emlen, 1973) and since the model parameters are life history

traits, it is possible to make a hypothesis about the relative importance of life history traits for the fitness (Schmidt & Lawlor, 1983). The more realistic the model is, the more accurate the prediction of the effect of an important trait on the fitness will be.

Another point that will be considered here, is the way in which separate life history traits act together to form a recognizable life history tactic (Stearns, 1976). In many cases models are used to explore the optimal combination of traits, using one or another measure of fitness. Several authors have pointed out that such models are unrealistic, in the sense that traits in them are assumed to be continuous and that various allometric constraints, that operate during the life of an organism, are not explicitly taken into account (Stearns, 1977, 1980; Watson, 1984). Recently it has become sufficiently clear that the shoot system of plants consists of discrete construction units or modules (Hallé et al., 1978; Harper & Bell, 1979; White, 1979). The consequence is that variation in life history traits might be discontinuous as well and a result of the use of meristems during the life of a plant (Watson, 1984). It is possible to define the optimal design of a plant in terms of the use of meristems (Smith, 1984); maybe it ultimately will be possible to define life history tactics in plants in terms of variation in the mechanisms that govern the formation and subsequent commitment of meristems to various functions.

In this paper two ecotypes of *Plantago lanceolata* L. will be used to illustrate the ideas in this introduction. Three questions will be addressed:

- What are the differences in life histories between two ecotypes of *P. lanceolata* from contrasting habitats? Hypotheses on the importance of several life history traits will be generated using a matrix model and sensitivity analysis.
- Are these differences really important in the field situation? Two tests will be used: an indirect test involving the genetics of life history traits and a direct one based on reciprocal transplanting.
- What switches exist in the design of *P. lanceolata* that control important differences in life history traits?

Plantago lanceolata is a rather short lived perennial rosette plant, which produces long stalked inflorescences from axillary meristems and can also give rise to side rosettes (Van Groenendael, 1985a). The flowers are born in spikes, each flower containing two ovules that need cross-fertilization. The plant is known to form distinct types in the field (Böcher, 1943; Primack, 1976; Teramura, 1978) and these differences are maintained under uniform conditions showing substantial genetic variation (Warwick & Briggs, 1979; Primack & Antonovics, 1981, 1982; Slim & Van der Toorn, 1982).

In the Netherlands *Plantago lanceolata* is found mainly in grassland habitats. Two habitats were selected that were strongly contrasting. Each of them has been more or less the same for at least a hundred years; this has probably provided a continuity in selective forces peculiar to each. The choice was based on the species composition of the habitats, being the most reliable indicator of habitat conditions (Westhoff & Van der Maarel, 1978). Ordination of all communities with *Plantago lanceolata* confirmed this choice and provided an objective measure 'of ecological distance' between the two habitats (Haecck et al., 1981). The first site is a dry and open dune grassland, grazed as commonage by cattle and horses for several hundred years (Noë & Blom, 1982). Occasionally and unpredictably the grassland suffers from catastrophic droughts in spring and summer. The second site is a permanently waterlogged, closed hay field, situated in a former river bed, now filled with a thick peat layer. The vegetation is mown once a year in July.

The population from the dry site is the shorter-lived of the two. It has a seedbank, juveniles and adults share the mortality risks equally and individuals show a tendency towards monocarpy. The other population is longer-lived, juveniles carry the greatest mortality risk, there is almost no seedbank and individuals are definitely iterocarpic (Table 1). Both life histories seem to be a response to the environment, being hazardous and unpredictable in the dry site and stable in the wet site.

Detailed field observations in permanent quadrats with mapped individuals over a three year period, provided information on age- and size-dependent mortality and fertility schedules. This large set of data has been summarized in a comprehensive matrix model (Van Groenendael & Slim, chapter 4). In the case of an iterocarpic perennial both size and age are important categories to describe the life cycle and therefore a modified version of the model proposed

Table 1. Characteristic differences between two populations of *Plantago lanceolata* from a dry dune grassland and a wet meadow, respectively.

	dry grassland		wet meadow	
	mean	CV%	mean	CV%
No. of leaves/rosette	6.6	27	3.8	25
Length of longest leaf (mm)	34	24	203	24
No. of ears/genet	9.2	69	1.7	47
Length of scape (mm)	54	61	380	29
Length of ear (mm)	7.3	31	17.1	34
No. of seeds/ear	15.74	75	57.17	53
Seed weight (mg)	0.73	75	1.91	39
No. of side rosettes/rosette	3.6		0	
% adults flowering	31		20	
% rosettes with side rosettes	12		0	
No. of seeds in the soil per m ²	1700		500	
No. of seedlings per m ² 1979	779		1158	
1980	486		465	
% germinating in spring 1979	68		44	
1980	75		46	
% seedlings surviving 1979 → 1980	59		26	
1980 → 1981	45		28	
Half-life adults in months	20		46	

by Law (1983) was used (Figs. 1 and 2). The main structure of the matrix is based on age, divided in years. The maximal number of years considered is three times the half-life of the population. Special categories have been created for autumn and spring cohorts of seedlings and their juvenile survival because of strong seasonal influences. Side rosettes are also treated separately, until the effects of season or mode of birth have subsided. Each matrix element is in itself a small matrix based on five size categories. All B elements contain mean number of offspring produced per age and per size category. All P elements contain survival probabilities per age and size, beginning with the probability of surviving from the moment of germination until the first census date, taken as the first of July. The numerical values for each element older

											Σ
B ₁		B _{2a}	B _{2s}	B _{2z}	B ₃	B _{3z}	B ₄	B _{4z}	B ₅	B ₆	N _{1a}
0.10	·	0.13	0.02	0.13	0.42	0.22	0.39	0.12	0.28	0.12	1.93
	B ₁	B _{2a}	B _{2s}	B _{2z}	B ₃	B _{3z}	B ₄	B _{4z}	B ₅	B ₆	N _{1s}
	0.17	0.21	0.03	0.23	0.72	0.37	0.66	0.21	0.47	0.20	3.27
		Z ₂	Z ₂		Z ₃	Z ₃	Z ₄	Z ₄	Z ₅	Z ₆	N _{1z}
		0.67	0.17	·	0.69	0.14	0.33	0.06	0.17	0.07	1.68
P _{1a}											N _{2a}
1.61	·										1.61
	P _{1s}										N _{2s}
	3.08										3.08
		P _{1z}									N _{2z}
		1.68	·								1.68
		P _{2a}	P _{2s}								N ₃
		1.43	2.86	·							4.29
				P _{2z}							N _{3z}
				1.32	·						1.32
					P ₃						N ₄
					2.46	·					2.46
						P _{3z}					N _{4z}
						0.59	·				0.59
							P ₄	P _{4z}			N ₅
							1.10	0.21	·		1.31
									P ₅		N ₆
									0.38	·	0.38
											<hr style="width: 100%; border: 0.5px solid black;"/>
											Σ 23.60

Figure 1. Goodman transition matrix for a population of *Plantago lanceolata* in a dune grassland. Each matrix element represents an age category and is in itself a matrix of size categories, not shown. Figures indicate relative sensitivities. Symbols are as follows: B number of seeds produced per age category; Z number of side rosettes produced per age category; P transition probabilities between age categories; N number of individuals per age category. Figures in subscript refer to years: 1 year of germination; 2 first year; 3 second year, etc. Letters in subscript refer to cohorts within years: a autumn cohort; s spring cohort; z cohort of side rosettes.

	B _{4a}	B _{4s}	B _{5a}	B _{5s}	B _{6a}	B _{6s}	B ₇	B ₈	B ₉	B ₁₀	B ₁₁	B ₁₂	N _{1a}
	0.02	0.01	0.10	0.05	0.11	0.05	0.17	0.16	0.13	0.11	0.09	0.03	1.05
	B _{4a}	B _{4s}	B _{5a}	B _{5s}	B _{6a}	B _{6s}	B ₇	B ₈	B ₉	B ₁₀	B ₁₁	B ₁₂	N _{1s}
	0.01	0.01	0.05	0.03	0.06	0.03	0.10	0.09	0.08	0.06	0.05	0.02	0.59
P _{1a}	1.05												N _{2a}
													1.05
P _{1s}		0.57											N _{2s}
													0.57
P _{2a}			0.95										N _{3a}
													0.95
P _{2s}				0.59									N _{3s}
													0.59
P _{3a}					1.04								N _{4a}
													1.04
P _{3s}						0.59							N _{4s}
													0.59
P _{4a}							1.00						N _{5a}
													1.00
P _{4s}								0.57					N _{5s}
													0.57
P _{5a}									0.85				N _{6a}
													0.85
P _{5s}										0.47			N _{6s}
													0.47
P _{6a}											0.68		N ₇
													1.10
P _{6s}												0.42	N ₈
													0.82
P ₇													N ₉
													0.82
P ₈													N ₉
													0.57
P ₉													N ₁₀
													0.37
P ₁₀													N ₁₁
													0.20
P ₁₁													N ₁₂
													0.06
													<hr/>
													Σ 12.44

Figure 2. Goodman transition matrix for a population of *Plantago lanceolata* in a wet meadow. Structure and symbols as in Fig. 3.

than three years have been inferred from the fate of adult individuals present at the beginning of the field observations. The other data come from cohorts of seedlings followed over time.

The matrices were solved numerically. The dominant eigenvalue is the population growth rate λ , the right eigenvector W gives the stable age/size distribution and the left eigenvector V gives the reproductive value of each age/size category. The scalar product of both vectors $\langle V, W \rangle$ is a measure for the mean length of generation (Leslie, 1966). For the two populations under study this demographic information is given in Fig. 3. Comparison between calculated and actual age/size distributions in July in the field gave a satisfactory fit (Van Groenendael & Slim, chapter 4). There are more small and young individuals in the wet site with a greater chance of dying than in the dry site. This results in an unexpectedly low mean length of generation for the population from the wet site. Field observations had led to the opposite impression, based on the longevity of adults. Judging from the reproductive values (Fig. 3), size is more important in the wet site: there is a greater reward for growing into size category 5. The same holds for growing old. The spring cohort in the wet site becomes gradually more important because of a better survival over time than the autumn cohort that faces heavy winter mortality when still small. The autumn cohort is more important in the dry site because it survives better the summer droughts. In this population side rosettes contribute significantly to the reproductive value especially when young.

A more comprehensive impression is given by the sensitivity analysis. The effect of small changes in any of the matrix elements a_{ij} on the population growth rate can be expressed as follows:

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle V, W \rangle} \cdot a_{ij}$$

A slightly different normalisation has been used in comparison with the original sensitivity measure of Caswell (1978). This brings out better the biological implications (De Kroon et al., submitted).

The results for both populations were calculated, summed over the size matrices, and are presented in Figs. 1 and 2. The sensitivities for size dependent seed production and survival are omitted for the sake of clarity, but size category 4 is most important for seed production when plants are young in the wet site and most important for all ages in the dry site. Again growing to category 5 in the first 4 years and staying there afterwards is most important in the wet site. Growing to category 4 in one year and staying in 4 is most

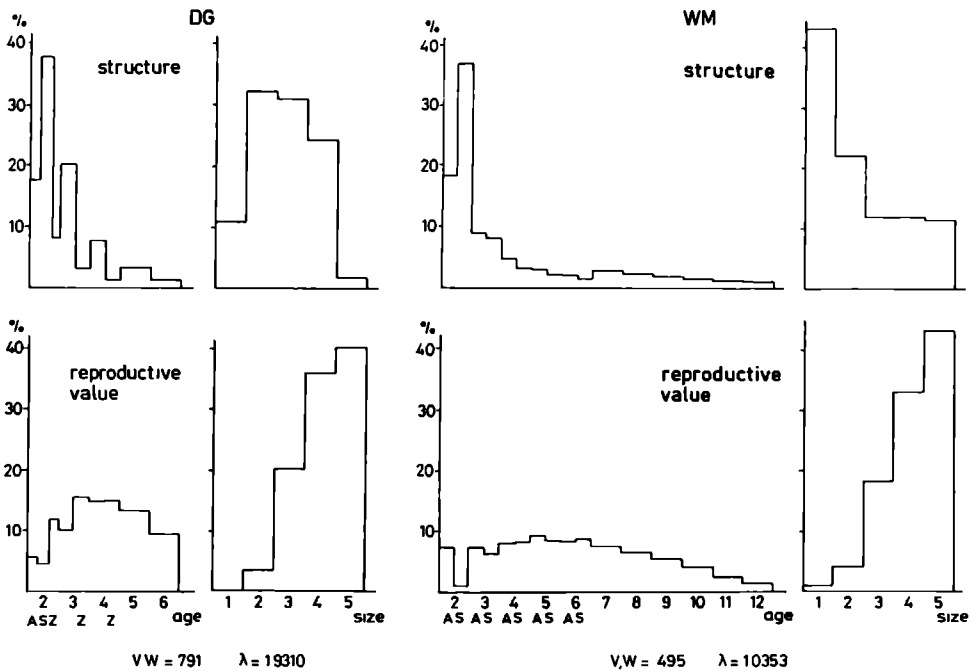


Figure 3. Limit properties of the Goodman transition matrices for the population of a dry dune grassland (a) and for the population of a wet meadow (b). Stable age and size structure and the reproductive value, given age and size, are shown. Letters refer to different cohorts within one year, until they are merged (A = autumn cohort, S = spring cohort and Z = cohort of side rosettes). Mean length of generation and population growth rate were 791 and 1,9310 respectively in the dry and 495 and 1,0353 for the wet population.

important in the dry site (for full details see Van Groenendael & Slim, chapter 4).

The following hypotheses can now be formulated, based on the model's properties and the sensitivity analysis, using Fisher's theorem:

- Germination and establishment are important phases in both life histories, but especially so in the dry site. Staying alive as an adult is relatively more important in the wet site. Considering that the greatest mortality oc-

curs in seed and seedling phases in the wet site, there is surprisingly small selective pressure in these phases. The death of a few adults seems as important as the death of many seedlings (see also Antonovics & Primack, 1982).

- The effect of a seedbank in the dry site is rather unimportant, but side rosettes are an important source of new recruits; their importance is mainly limited to the first year.
- Immediate germination in autumn is most important in the wet site; delayed germination in spring is most important in the dry site. This is confirmed by the actual germination pattern in the field. It should be noted, however, that the other cohorts still have relatively high reproductive values, which may account for the existence of the two germination flushes.

TESTS OF LIFE HISTORY HYPOTHESES

Two kinds of experiments have been proposed to test the hypotheses given in the previous section. Reciprocal transplanting of ecotypes has been strongly advocated (Antonovics & Primack, 1982) because it allows direct comparison of different life histories in terms of fitness, by recording fitness parameters such as survival. In such transplant experiments, the subsequent phases of the life cycle should be investigated as completely as possible. Three phases of the life cycle of *Plantago lanceolata* were tested: The survival of seeds in the soil, the germination and subsequent survival of seeds and seedlings and the growth and survival of young adults.

The other test used, is the more common one of growing plants from the different sites under uniform conditions to establish the genetic basis of the differences between various morphological features which may be related to the life history traits we are interested in.

Reciprocal transplant experiments

The first phase tested by reciprocal transplanting was the fate of seeds in the soil. After burying seeds in nylon mesh tubes in the autumn of 1979, survival was tested by retrieving a set of tubes every three months and testing the surviving seeds for viability. Apart from site and origin, seed size and depth of burial were explicitly taken into account. A total of 4,800 seeds

were tested this way. Time, depth of burial and relative seed size are major determinants of the survival of seeds in the soil, but there were minor but significant site effects and effects of origin (Van Groenendael, 1985b). Seeds from both populations survive better in the dry site and seeds from the dry site do better in both habitats (Fig. 5A). The interaction between site and origin, which suggests local adaptation, is significant only after taking into account the effects of size or depth of burial. The contrast is mainly a result of high mortalities in the wet site for seeds from the dry site when buried deep or when small. The seeds from the wet site are less affected by the contrast in environment. They show a more uniform survival pattern.

In the second phase germination and establishment were investigated. Marked seeds were sown in replicate plots in a cm grid in the spring of 1979. After germination seedlings were followed over time. The survivors were measured at regular intervals. In total 3,200 seeds were sown. All germination takes place in one season in the wet site, whereas there is delayed germination in the dry site (Fig. 4). The timing of the germination, represented by the shape of the curves, shows a strong environmental control, regardless of origin, except

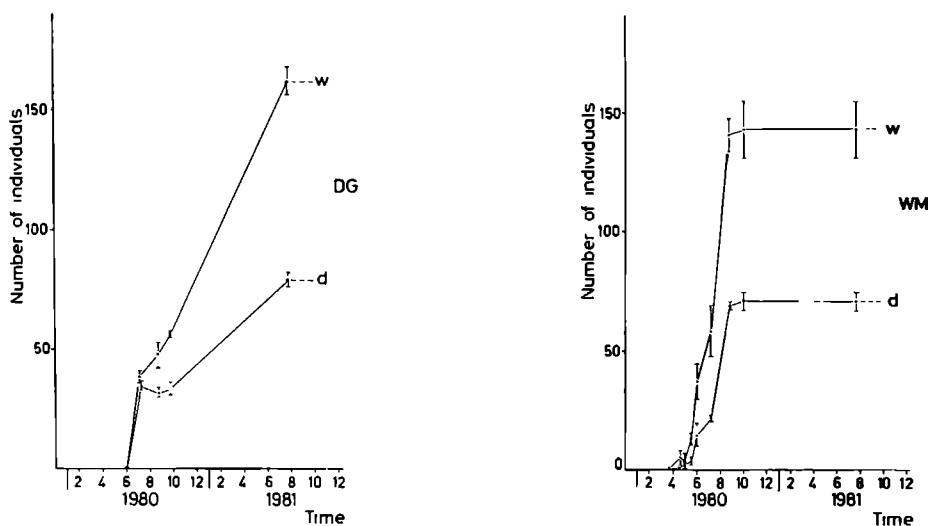


Figure 4. Germination of seeds from dry grassland (d) or wet meadow (w) transplanted into the dry grassland (DG) or into the wet meadow (WM).

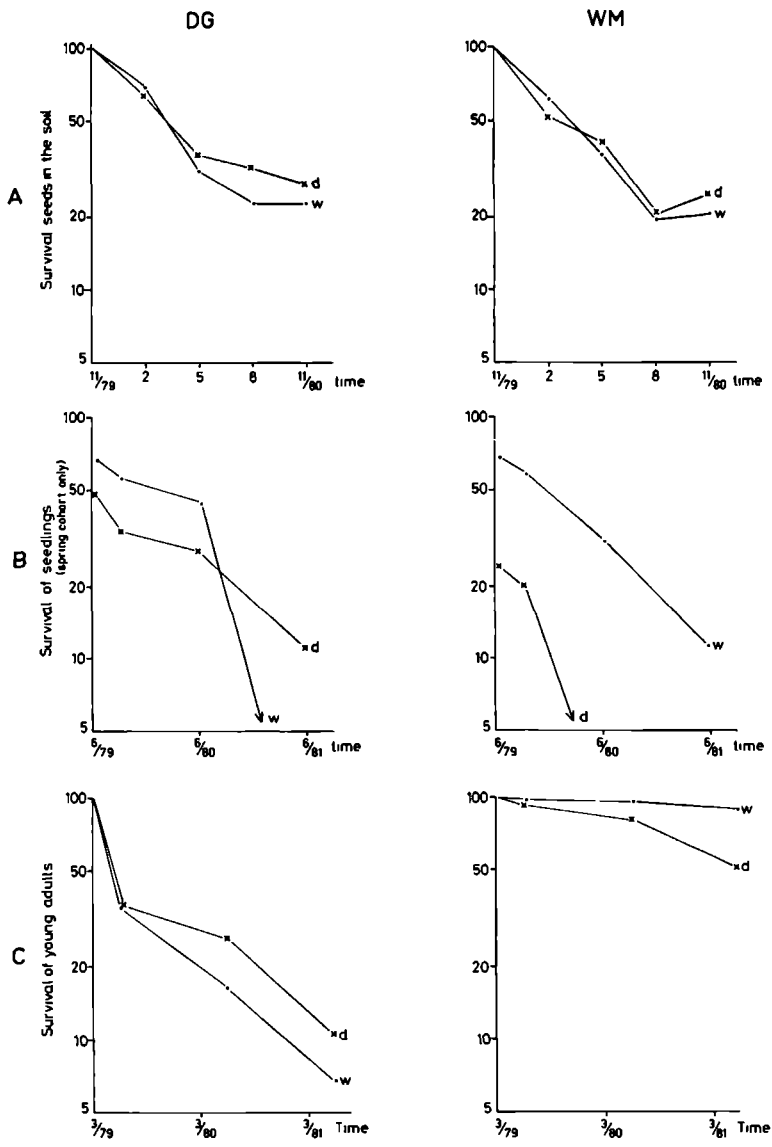


Figure 5. Survivorship curves of various experimental cohorts (A, B, C) of two populations of *Plantago lanceolata* originating from a dry grassland (d) or from a wet meadow (w) transplanted reciprocally into the dry grassland (DG) or into the wet meadow (WM).

for a somewhat retarded start in the wet site for seeds from the dry site. This can be explained by a greater sensitivity to lower temperatures for germination for seeds from this site, found under standard laboratory conditions (unpublished results). The total number of seeds that germinate is strongly affected by the origin of the seeds and to a lesser extent by site effects, but there is no significant interaction term in the analysis of variance (Van Groenendael, 1985b). This points at a rigid control over the level of germination. After germination the seedlings from the wet site do establish significantly better than the seedlings from the dry population in both habitats (Fig. 5B). There is a weaker, but still significant site effect, due to better establishment in the dry site. However, it is not until the first period of drought in the spring of the second year that interaction becomes evident, with each ecotype performing best in its own habitat and the strongest contrast for the young adults from the wet site.

The last part of the life cycle that was investigated was juvenile and adult survivorship, using shoots propagated vegetatively from leaves (Wu & Antonovics, 1976) collected from flowering individuals in the field. Each site was represented by 10 genotypes and 20 shoots per genotype were used for reciprocal transplanting in a randomized block design in the spring of 1979 in both habitats. Survival was recorded at regular intervals over a two year period. Strong site effects dominate the first few months, due to an early spring drought (Fig. 5C). After the first year interaction became significant, again with the strongest contrast in survival for plants from the wet site. Comparison of survival of individual genotypes between sites, using a χ^2 -analysis, showed no significant differences between genotypes from the wet site. They all reacted very uniformly on the contrast between the sites, indicating genetic homogeneity. Between the genotypes from the dry site, however, there were significant differences in survival pattern between the sites, suggesting stronger genetic heterogeneity (Van Groenendael, 1985b).

When comparing these results with the predictions from the model, one can see similarities. When there is strong selective pressure, local specialization is expected and this is reflected in the analyses of variance in strong interaction terms in the survival parameters, being the ultimate test for the fitness in these experiments. A strong contrast is found for adult survival in plants from the wet site, indicating strong selective pressure, also predicted in the model. No strong selection was apparent in survival of seeds in the soil, confirming the model's prediction. The weak interaction terms, however,

point in the direction of a stronger contrast for the seeds from the dry site. When the seedbank is considered to be a way to increase the establishment of new recruits, this again is in accordance with the model.

There are, however, two drawbacks in this reciprocal transplant experiment. The first is, that only in the long run is the test really reciprocal, after all the hazards of life have been encountered. In the short term there might be a severe imbalance in the reciprocity. For instance, the big seeds from the wet site germinate readily and, without competition, grow fast in the dry site. At the same time seedlings from the dry site suffer from shading in the wet habitat. Full reciprocity is achieved, only after periods of drought. Until then, there is a wrong estimation of local adaptation. The second point is, that it is usually not clear how this local adaptation in survival is achieved, whether by genetic canalization or by plasticity and through what traits. As an example, the effects of seed size will be discussed. The seeds from the dry site are small and very variable (Table 2). They are produced

Table 2. Variability in two traits under controlled conditions and in the field for both populations of *Plantago lanceolata*.

	greenhouse		field	
	mean	CV%	mean	CV%
Seed weight DG	1.32	46	0.73	75
Seed weight WM	1.71	29	1.91	39
Length of cotyledon DG	25.70	32	13.17	37
Length of cotyledon WM	42.10	24	23.40	53

under conditions. When grown in the laboratory, there is a substantial gain in seedweight and a reduction in variability, but with a considerable amount of variability still left. In the field there is a significant negative correlation between the number of seeds per mm of spike and the weight of the seed ($r = -0.4490$, $p < 0.01$, $n = 28$). This suggests a trade-off between number of seeds and the individual size of a seed. Seed size is far more strictly regulated in the wet meadow population, showing the opposite tendencies and no significant correlation ($r = 0.2135$, n.s., $n = 30$).

Seed size in turn, determines the length of the cotyledons, being bigger for the wet meadow population. The cotyledons in this population are also more variable in the field. This variability is mainly phenotypic and strongly reduced under laboratory conditions (Table 6). It is easy to see the advantage of such variability, because it enables these seedlings to reach the light in a dense vegetation. There is a significant positive correlation between the length of the cotyledons and the growth in the first three months in the field, irrespective of the habitat ($r = 0.6368$ in the wet site and $r = 0.6407$ in the dry site, $p < 0.01$, $n = 20$). No such correlation exists for the dry population ($r = 0.3456$, $n = 17$ and $r = 0.0421$, $n = 19$, respectively, both non significant).

The conclusion is, that variability in seed size and relative constancy in the seedlings developing from them, permits the dry population to establish enough seedlings. In the wet habitat such variability is fatal. Constancy in seed size and plasticity in seedlings, on the other hand, gives the seedlings from the wet population at least a chance in a competitive environment. In a non-competitive environment and in combination with a high and constant growth rate, plants grow too big to withstand periods of drought. (The relative growth rates after six weeks were 155 and 145 mg/g/day for the wet and dry site populations respectively; the coefficients of variation were 0.28 and 0.51 respectively).

Laboratory test

To elaborate the point of selective pressure on the variability of traits somewhat further, the following experiment has been done. Three plantlets from the clonally propagated genotypes from the last experiment were saved and grown to flowering in the greenhouse. Several morphological traits were measured and analysed in a nested analysis of variance. This permits not only a comparison between origins but also a comparison of the between-genotype component of variance with the within-genotype component of variance. The resulting F-value is presented in Table 3. As far as these variance ratio's represent an estimate of the heritability of the traits measured, albeit an over-estimate, this is an indication of the genetic 'control' over a trait. The coefficient of variation in combination with the F value indicates how variable a trait is under controlled conditions and whether this variability is genetically controlled or the result of plasticity. At the population level there are signi-

ficant differences in all eleven traits measured, which confirms the distinctness of the two ecotypes. In general on the genotype level, more traits show significant variance ratio's in the wet than in the dry site.

Looking in more detail and grouping traits into two categories, one related to the production of offspring and the other related to the size of an adult (labels 1 and 2 in Table 3, respectively) it becomes clear that the variance ratio's are higher in adult size characteristics than in traits re-

Table 3. Mean, coefficient of variation and F-ratio for between versus within genotype variance for several morphological traits of two *Plantago lanceolata* populations, measured in clonally propagated offspring from 10 flowering adults from each habitat grown in the greenhouse. Superscripts refer to traits related to size (1) and to the production of offspring (2).

	dry grassland				wet meadow			
	mean	CV%	F	p	mean	CV%	F	p
¹ Length longest leaf cm	12.5	28	4.55	0.01	20.1	23	11.30	0.001
¹ Width longest leaf mm	13.8	42	2.82	0.05	20.6	32	4.49	0.01
¹ Length longest scape cm	39.2	20	6.88	0.001	53.2	16	4.46	0.01
¹ Estimated biomass	242	82	2.07	0.1	647	50	4.26	0.01
² No. of leaves	12.9	31	2.87	0.05	15.0	18	2.06	0.1
² No. of spikes	28.3	44	1.76	ns	6.3	63	11.50	0.001
² No. of side rosettes	9.2	48	5.86	0.001	1.9	118	3.82	0.01
² Length longest spike mm	28.0	25	9.07	0.001	39.8	32	6.46	0.001
² No. of seeds per spike	52.9	40	12.15	0.001	92.3	36	1.45	ns

lated to reproduction in the population from the productive, closed hay meadow. The reverse is true for the population from the dry and open dune grassland: Here the variance ratio's are higher in traits related to reproduction and lower in traits related to adult size. Also when there is a significant genetic control, the variability is relatively lower in size related traits than in traits related to reproduction in the wet population and lower in traits related to reproduction than in traits related to size, but less markedly

so for the dry population. These observations on the total genetic variance are not conclusive with respect to the predictions of the model, but they are certainly along the lines predicted for the additive genetic variance. Apparently traits are under more strict genetic control in the wet site than in the dry site and have low variabilities, when traits related to adult size are considered. Exactly those traits were expected to be under selective pressure according to the model. The variability in traits in the dry site was more plastic especially in size related traits. There was a higher genetic control in traits related to reproduction and the variability was also somewhat lower in these traits, where, according to the model, the higher selective pressure was expected.

THE IMPORTANCE OF ARCHITECTURE

The conclusion from the previous section is that the differences between the two populations have a genetic basis and that the differences seem to be adaptive. Most likely they cannot survive in each others habitat. The predictions from the model are borne out quite well, confirming the usefulness of such a matrix model in an evolutionary context.

On the basis of the model certain life history traits have been identified that could be responsible for these differences in fitness. Adult survival was the most important trait for the population from the wet site. In this phase the population proved to be most sensitive to a change in the environment because of narrow genetic specialization, directed at maintaining adults in a competitive environment. Adults from the population of the dry site proved to be more heterogeneous and less affected by the contrast. This heterogeneity is necessary to survive in a hazardous environment. Juvenile survival, however, was more important for this population, which is geared towards producing enough offspring, regardless of the size of individuals and releasing them slowly into the environment. This variability prevents establishment in a competitive environment. Seed and seedlings from the wet site proved to be more homogeneous and their establishment was hardly affected by the contrast in the environments.

It is clear that the whole of the life history traits determines the fitness of a population. Such a combination of life history traits has been described as a 'life history tactic' (Stearns, 1976) or as a 'plant strategy'

(Grime, 1979) and is defined as a set of co-adapted traits, that are inherited as such. Although there is some proof for the existence of genetic correlation for life history traits (Etges, 1982), it remains difficult to see how such correlation has been generated by selection. One solution could be, that there exists a more simple and more general underlying structure which regulates a set of traits at the same time and on which selection can operate. A possible candidate for such a general, underlying regulator is the way the growth of a plant is controlled. When growth is expressed not merely in terms of dry weight, but in terms of the dynamics of plant parts it becomes possible to describe the size as well as the shape of a plant. Plant size and plant form can be viewed to be regulated by variation in the number of units, in the size per unit and in the use of different orders of meristems (Van Groenendael, 1985a).

With regard to the two ecotypes of *Plantago lanceolata*, used in this study, the major differences in life history tactics can now be related to differences in modular growth. In the wet site it is important to maintain a large main rosette, to be able to compete with other tall grasses and forbs. In terms of modular growth this means a slow initiation of new modules (short internode, with a leaf attached to it and an axillary meristem) in the main rosette so that each unit can grow big enough. It also means a tight control over the use of the axillary meristems, so that no side rosettes are formed and only a few ears, that again can grow big. In the dry site it is important to produce many offspring. This can be achieved by a rapid production of small leaves in the main rosette. The axillary meristems associated with the leaves then produce side rosettes, causing a rapid proliferation of growing points, and many inflorescences in the main as well as in side rosettes.

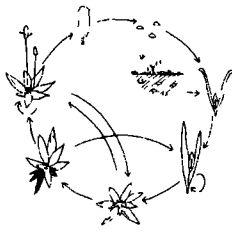
A large part of the differences noticed in the life histories of the two populations of *P. lanceolata* from contrasting habitats can be reduced to two fundamental controls: control over the speed of initiation of new modules or plastochron time in the main rosette and control over the induction of second order meristems. These two controls define the form of the plant and the way its resources will be allocated. It offers a way to understanding life history tactics not only in terms of co-adaptation of traits but also on a deeper level of regulation, affecting several life history traits at once.

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SUMMARY

It has been the aim of this study to demonstrate the validity of certain aspects of what is commonly referred to as the 'life history theory'. The central tenet of this theory is the existence of sets of co-adapted life history traits, which together make up a so-called life history tactic, selected as such as a result of particular environmental conditions. The relevance of this theory is that evolution is taking place through differences in life history traits such as age- and size-dependent reproduction and survival, longevity and time to first reproduction. Knowledge of any co-adapted pattern in life history traits would therefore improve our understanding of the process of evolution.

In order to test the theory, empirical information was collected on the life histories of two ecotypes of *Plantago lanceolata* L. (Ribwort Plantain), mainly based on a demographical analysis over a three-year period. Ecotypes from one species were chosen because several authors considered ecotypes to provide the best opportunity for comparison of differences in life histories. The habitats of these ecotypes were selected for their contrast in density-dependent regulation, as this is a central concept in the theory. The first habitat was an open dry dune grassland on leached, nutrient-poor, sandy substratum, which had been in use as a commonage continuously for several centuries. Its vegetation is open, with little above-ground interference, and it suffers from occasional but unpredictable droughts. The second habitat was an old, productive hay meadow on a completely organic, permanently waterlogged substratum, which fills a medieval river bed. Its vegetation is dense, with many species, and is mown once a year in mid-July. Two distinct ecotypes of *Plantago lanceolata* are found in these habitats, differing in morphology as well as in life history. The dry ecotype, described in taxonomic literature as subvar. *sphaerostachya* Mert. et Koch f. *minor*, has small, flat rosettes with many leaves and many globular inflorescences on short ascending stalks. Frequently, side rosettes are formed from axillary meristems that serve to maintain the genet and enlarge its seed output in the current year. Many small seeds are produced which show innate dormancy, resulting in a spring flush of seedlings. Light and temperature requirements of the germination are such that there exists some enforced dormancy resulting in a substantial seedbank. Individuals in this population reproduce early in life, but they are short-lived. Juveniles and adults share about equal mortality risks and the population growth rate is high. The wet ecotype, described as subvar. *latifolia* Wimm. et Grab., is a much taller plant, with few

tall erect leaves, one or two oblong inflorescences on long straight stalks and no side rosettes. Fewer but bigger seeds are produced in comparison with the dry ecotype, and these seeds do not show any dormancy and do not form a substantial seedbank. After germination, individuals of this population show high relative growth rates under optimal conditions, but growth is slow in the field because of shading, and consequently many seedlings and juveniles die. Adults, on the contrary, are long-lived and flower repeatedly. The combination of high juvenile mortality and low adult mortality results in a low population growth rate.

The life histories described in this study show a clear pattern, which is in accordance with predictions from life history theory. A high population growth rate, early reproduction, short life-span, many small seeds, a seedbank, vegetative spread, reduced iterocarp, equal mortality risks for juveniles and adults, all these have been mentioned by several authors in connection with unpredictable environments with density-independent regulation of population size. The reverse is true for stable environments, showing density-dependent regulation. However, a satisfactory fit between actual life histories and the life histories expected on the basis of habitat characteristics, does not constitute sufficient proof for the validity of the life history theory. Two further points must be established; firstly, that differences in life history traits result in differences in fitness and, secondly, that these traits are co-adapted, forming together a life history tactic. As to the first point, two methods have been used to test the adaptive significance of differences in life history traits; a direct one using reciprocal transplant experiments, and an indirect one using sensitivity analysis in descriptive population models, based on matrix projection techniques.

In the first test individuals of both populations were transplanted reciprocally into their own and the other habitat, in three distinct phases of the life cycle. Survival of seeds buried in the soil was recorded in a reciprocal burial experiment. Germination and subsequent establishment was followed in a reciprocal sowing experiment, and adult survival was registered using clonally propagated offspring from successful genotypes in the original habitats. In all three experiments there were significant site and origin effects, but also significant site x origin interactions in the direction of a better performance in the home site. This points at local specialization. After a sufficient period of time for the habitat differences to take full effect, it can be concluded that both populations, summed over their whole life cycle, are unfit to

survive in each other's habitat. An attempt was made to relate the differences in fitness between the genotypes in the adult transplant experiment to specific morphological traits, measured for the same genotypes grown in the greenhouse. In general there were only weak correlations between any of the traits measured and the individual fitness of the genotypes in both field habitats, except for the number of leaves in the main rosette. On the whole there was greater plasticity in morphological traits in the genotypes from the dry site than in those from the wet site, but, regardless of origins, the most plastic genotypes had the lowest fitness when growing in the stable, wet habitat. This suggests that plasticity is important in defining an individual's fitness.

The second test involved the simulation of the population dynamics of both populations, based on the demographical data, using matrix projection models. The fecundity and survival parameters that together form the matrix elements, were evaluated for both size and age categories at the same time, using the formulation originally proposed by Goodman. The output of the model was verified against field data and this proved to be satisfactory. After this verification both absolute and relative perturbations were applied to the matrix elements and their effect was registered on the population growth rate, which is the dominant eigenvalue of the matrix. From this perturbation or sensitivity analysis it could be concluded that the population dynamics in the dry site depended most clearly on new recruitment, whereas adult survival was most important in the wet site. There is no doubt about the usefulness of this matrix model in summarizing large data sets. Apart from this capacity, sensitivity analysis of the model can generate a large array of hypotheses. It was expected for instance, that the greater sensitivity of recruitment or adult survival would be reflected in a greater selective pressure on these traits or on traits directly affecting recruitment or adult survival, resulting in local specialization and low levels of additive genetic variance. Local specialization was evident in all three reciprocal transplant experiments, but in the case of the dry population, the contrast in performance between home site and alien site was most obvious for the survival of seeds in the soil, while for the wet population this contrast was most marked for adult survival in the adult transplant experiment. This confirms the expectations from the model. Further support comes from the fact that those morphological traits that are related to the production of offspring, e.g. number of inflorescences, number of seeds per ear, number of side rosettes, were generally less variable in the dry population and more strictly controlled. The same is true for the wet population for

those traits that are related to competitive ability as the major factor in maintaining adult rosettes, e.g. length and width of leaves and biomass.

As to the second point, whether life history traits are co-adapted to form a life history tactic, this has not been tested explicitly. However, in one way or another, a more general principle, open to selection, must underlie such a set of life history traits. The control over meristematic activity during plant morphogenesis could be such a principle. It is suggested that the different morphologies of individuals of the two populations of plantains can be reduced to two underlying characteristics, one being the control over the speed of initiation of new leaves in the main rosette or plastochron time, and the other being the control over the induction of the axillary meristems associated with the leaves in the main rosette. These two controlling mechanisms determine whether a plant will grow tall with few big leaves and inflorescences or whether it will remain small with many leaves, many small inflorescences, and a rapid proliferation of growing points because of side rosettes arising from axillary meristems, which produce inflorescences as well. In fact those two controlling mechanisms determine not only the form of the plantain rosette but also the way its resources will be allocated. This offers a way to understanding life history tactics not only in terms of co-adaptation of traits but also on a deeper level of regulation, affecting several life history traits at once.

SAMENVATTING

Het doel van dit proefschrift is de geldigheid te onderzoeken van een aantal uitspraken die zijn gebaseerd op de zogenaamde "strategie-theorie". De centrale veronderstelling in deze theorie is het bestaan van onderling op elkaar afgestemde en ook samen geselecteerde kenmerken van een levenscyclus, die samen een overlevingsstrategie vormen als reactie op bepaalde factoren in het milieu. Het belang van deze theorie is, dat evolutie plaatsvindt juist door verschillen in kenmerken van de levenscyclus, zoals voortplanting en overleving, levensduur en de tijd nodig om tot voortplanting te komen. Kennis van enig door selectie te- weeggebracht patroon in de levensverrichtingen zou daarom ons inzicht in het evolutieproces vergroten.

Om de theorie te testen, zijn gegevens verzameld over de levenscyclus van twee oecotypen van *Plantago lanceolata* L. (smalle weegbree), voornamelijk geba- scerd op demografisch veldwerk gedurende drie achtereenvolgende jaren vanaf 1979. Aan oecotypen van één soort is bij de bewijsvoering de voorkeur gegeven, omdat deze algemeen worden beschouwd als het beste uitgangsmateriaal om ver- schillen in levenscyclus te onderzoeken. De terreinen waar deze oecotypen voor- komen, zijn uitgekozen op grond van hun verschil in dichtheidafhankelijke re- gulating van de populatiegrootte, omdat deze afhankelijkheid een centraal begrip in de theorie is. Het eerste terrein is een open en droog duingrasland op voed- selarm, zandig substraat. Het grasland wordt al enkele eeuwen gebruikt als ge- meenschappelijke weide en begraaasd met vee. De vegetatie is open, met weinig bovengrondse wisselwerking tussen planten, en is onderhevig aan af en toe op- tredende droogteperioden. Het tweede terrein is een hooiweide in een verlande rivierarm. De bodem is zuiver organisch en permanent met water verzadigd. De vegetatie is hoog, gesloten en soortenrijk en wordt eenmaal per jaar gemaaid, en wel half juli. In deze twee terreinen worden twee duidelijk van elkaar ver- schillende oecotypen van de smalle weegbree aangetroffen.

Het oecotype van droog milieu, dat in de taxonomische literatuur wordt aan- gedeut als subvar. *sphaerostachya* Mert. et Koch f. *minor*, heeft kleine vlakke rozetten met veel blaadjes en ronde bloeiwijzen op korte opstijgende stelen. Regelmatig worden zijrozetten gevormd uit okselmeristematen, die bijdragen tot een langere levensduur van het individu en tevens tot een hogere zaadproduktie. Een groot aantal kleine zaadjes wordt gevormd, die een aangeboren kiemrust ver- tonen, zodat de meeste kieming pas optreedt in de lente. De kieming is geringer

in het donker en verloopt pas optimaal bij tamelijk hoge temperaturen, met het gevolg dat lang niet alle zaden kiemen en dat er een zaadvoorraad aanwezig is in de grond. De rozetten in deze populatie kunnen al in het tweede seizoen bloeien, maar in het algemeen is hen maar een kort leven beschoren. Jonge en oudere planten dragen ongeveer gelijke risico's en de populatiegroeisnelheid is hoog.

Het oecotype van vochtig milieu, beschreven als subvar. *latifolia* Wimm. et Grab., vormt veel forsere rozetten, met enkele lange en rechtopstaande bladen en één of twee cilindervormige bloeiwijzen op lange, rechte stelen. Er zijn maar zelden zijrozetten aanwezig. In vergelijking met het "droge" type worden er minder maar wel forsere zaden gevormd. Deze zaden vertonen nauwelijks kiemrust en kunnen kiemen bij lage temperaturen zonder remming in het donker. Daardoor valt de voornaamste kiemgolf al in het najaar en wordt er in de grond nauwelijks een zaadvoorraad gevormd. Na de kieming kunnen rozetten van de smalle weegbree uit deze populatie onder optimale condities snel groeien, maar in het veld is de groei echter traag als gevolg van overschaduwning. Vele kiemplanten en juvenielen sterven dan ook. Zij lopen duidelijk meer risico dan de volwassen planten, die lang blijven leven en, als ze eenmaal tot bloei zijn gekomen, vaker kunnen bloeien. De combinatie van hoge jeugdsterfte en lage adultsterfte van volgroeide planten resulteert in trage populatiegroei.

De levensstrategieën die in het veld zijn beschreven, zijn in overeenstemming met de theorie. Een hoge groeisnelheid van de populatie, een vroege reproductie, een kort leven, veel kleine zaden, het bezit van een zaadvoorraad, vegetatieve verbreiding, een beperkt aantal keren voortplanten, gelijke sterfterisico's bij jonge en oude rozetten, zijn evenzovele kenmerken van de levenscyclus die door diverse auteurs in verband zijn gebracht met onvoorspelbare milieus, waarin een van de dichtheid onafhankelijke regulatie van de populatiegrootte een belangrijke rol speelt. Het omgekeerde gaat op voor stabiele milieus met van de dichtheid afhankelijke regulatie. Een redelijke overeenkomst tussen enerzijds de levensloop zoals die zich voltrekt in het veld en anderzijds de voorspelde kenmerken van de levensloop, afgeleid uit de theorie op basis van bepaalde milieu-kenmerken, vormt echter nog geen voldoende bewijs voor de geldigheid van de theorie. Twee punten moeten verder nog worden vastgesteld: Allereerst of verschillen in kenmerken van de levenscyclus bepaalde individuen bevoordelen ten opzichte van andere, zodat selectie mogelijk is, en ten tweede, dat deze kenmerken samen geselecteerd zijn tot een levensstrategie. Ter beantwoording van de eerste vraag zijn twee wegen gevolgd om aan te tonen dat de

gevonden verschillen in levensloop ook werkelijk van voordeel zijn bij het overwinnen van de problemen in het eigen milieu. De eerste weg is het rechtstreeks in elkaars milieu overplanten van individuen. De tweede weg is indirect en maakt gebruik van een gevoeligheidsanalyse van populatiemodellen, die zijn gebaseerd op matrix-projectietechniek.

Bij het overplanten van individuen is gebruik gemaakt van drie afzonderlijke fasen in de levensloop: De overleving van begraven zaad is geregistreerd; kieming en vestiging zijn gevolgd na inzaai en tot slot is de overleving nagegaan van adulten, die waren verkregen door het klonen van planten die zich gevestigd hadden in de oorspronkelijke milieus. In alle drie de experimenten bleek zowel het milieu alsook de herkomst van de individuen van grote invloed op het succes van de individuen. Er was echter ook sprake van een duidelijke interactie tussen herkomst en milieu, hetgeen wil zeggen dat succes vooral optreedt in het eigen en niet in het vreemde milieu. Dit wijst op lokale specialisatie en selectie. Als de resultaten van de drie levensfasen bij elkaar worden gevoegd, moet de conclusie zijn, dat geen van de twee populaties in staat moet worden geacht te overleven in het andere milieu. Bij een poging verband te leggen tussen kenmerken van de levensloop en een aantal morfologische kenmerken, is alleen een betekenisvol verband gevonden tussen overleving in het droge milieu en het aantal blaadjes in het hoofdrozet. Over het geheel genomen bleek wel dat individuen van het droge milieu een grotere plasticiteit bezaten in morfologische kenmerken dan die uit het natte milieu, en dat juist die plasticiteit een nadeel betekende in het natte milieu, ook als die werd aangetroffen bij individuen uit dat milieu. Dit duidt op aanpassingswaarde van plasticiteit.

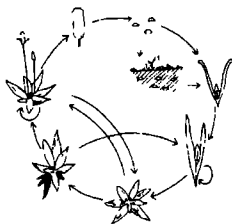
De tweede test had betrekking op het nabootsen van de populatiegroei van beide populaties met behulp van matrix-projectiemodellen. De vruchtbaarheid en de overlevingskansen, die samen de projectie-matrix vormen, zijn daarin ingevuld, rekening houdend met grootte en ouderdom van de rozetten, gebaseerd op de veldgegevens. De resultaten uit het model bleken redelijk overeen te komen met de veldresultaten. Na deze verificatie zijn zowel absolute als relatieve verstoringen aangebracht in de matrix-elementen. Geregistreerd werd het effect daarvan op de groei van de populatie, dat wil zeggen op de dominante eigenwaarde van de matrix. Op basis van deze zogenaamde gevoeligheidsanalyse kon geconcludeerd worden, dat de groei van de populatie in het droge duingrasland vooral afhangt van de jaarlijkse aanvulling met nieuwe rozetten, terwijl deze in de natte hooiweide veel meer afhangt van het in leven blijven van volwassen rozetten. Het is duidelijk dat dit soort matrixmodellen in staat is grote aantallen ge-

gevens op zinvolle wijze samen te vatten. Met de gevoeligheidsanalyse kan de populatie kritisch worden doorgelicht en kunnen nieuwe hypothesen worden opgeworpen. Zo kan men bijvoorbeeld het volgende verwachten. Als het zwakke punt in deze populaties ligt in de mate van aanvulling met nieuwe rozetten, of juist in de overleving van volwassen planten, dan zal dat resulteren in een versterkte selectiedruk op kenmerken, die van invloed zijn op deze zwakke schakels in de levenscyclus. Dit moet dan leiden tot lokale specialisatie. Lokale specialisatie was reeds aangetoond in de transplantatie-experimenten, maar de sterkste specialisatie bij de "droge" populatie werd gevonden voor overleving van zaad in de grond, terwijl bij de "natte" populatie het grootste contrast voorkwam bij de adult-overleving. Dit bevestigt voornoemde hypothese. Deze wordt verder nog ondersteund door het feit dat juist die morfologische kenmerken, die van invloed zijn op het voortbrengen van nageslacht (zoals aantal bloeiwijzen, aantal zaden per aar, aantal zijrozetten), in de "droge" populatie een lagere genetische variabiliteit vertoonden, hetgeen uitgelegd kan worden als een gevolg van selectiedruk. Iets dergelijks is ook gevonden in de "natte" populatie maar dan bij kenmerken die van invloed zijn op het overleven van volgroeide rozetten, zoals grootte van de bladen en de hoeveelheid gevormde biomassa.

Het bewijsmateriaal dat in dit proefschrift is aangevoerd laat geen uitspraken toe over de vraag of er sprake is van samen geselecteerde kenmerken, die een herkenbare levensstrategie vormen. Wel kan men speculeren over het mechanisme waarmee een samenhang tussen kenmerken van de levenscyclus tot stand komt. Dit zou kunnen, doordat een meer algemeen kenmerk ten grondslag ligt aan een aantal kenmerken van de levenscyclus. Er zijn aanwijzingen dat een dergelijk meer algemeen kenmerk met directe gevolgen voor andere kenmerken van de levenscyclus, is gelegen in de controle over aanleg en gebruik van meristematisch weefsel. De sterk verschillende uiterlijke verschijningsvormen van beide oecotypen van de smalle weegbree, kunnen uiteindelijk worden herleid tot mogelijkwerwijs twee basiskenmerken. Het eerste is de snelheid waarmee nieuwe bladen worden gevormd in het hoofdrozet en het tweede is de controle over het gebruik van de meristemen in de oksels van die bladen. Het eerste kenmerk bepaalt of er weinig maar grote bladen worden gevormd of juist veel, kleine bladen. Het tweede bepaalt uit hoeveel bladoksels bloeiwijzen zullen ontstaan of ook zijrozetten, die zelf weer bijdragen tot een snelle toename van het aantal okselmeristemen. In feite bepalen deze twee kenmerken de manier waarop het individu zijn vorm verkrijgt en daarmee ook de manier waarop de diverse (schaarse) hulpbronnen worden verdeeld over de plant. Indirect worden zo de diverse levensverrichtingen in samenhang gereguleerd en dit kan leiden tot een beter inzicht in levensstrategieën en tot verbetering van de strategie-theorie.

CURRICULUM VITAE
JAN MARIE VAN GROENENDAEL.

- 17-9-1945 Geboren te Maastricht.
- 1957 - 1963 Gymnasium β doorlopen aan het Henric van Veldeke College te Maastricht.
- 1963 - 1968 Studie scheikunde aan de Katholieke Universiteit te Nijmegen. Niet afgerond.
- 1969 Militaire dienst.
- 1969 - 1971 Leraar natuurkunde aan het Canisius College te Nijmegen.
- 1971 - 1978 Studie biologie aan de Katholieke Universiteit te Nijmegen. Kandidaatsexamen B1g afgelegd in januari 1974; doctoraal-examen afgelegd in mei 1978 (cum laude). Het doctoraalvakkenpakket was als volgt samengesteld:
Hoofdvak geobotanie, bestaande uit een plagexperiment op de Strabrechtse Heide o.l.v. drs. H. Helsper en een onderzoek naar de invloed van de zee op de vegetatie van meren en moerassen in West-Connemara, Ierland o.l.v. prof.dr. V. Westhoff en prof. J. Moore, Dublin University.
Eerste bijvak bodemkunde. Hierin is een analyse uitgevoerd van bodem- en plantmonsters t.b.v. eerste deel van het hoofdvak o.l.v. drs. A. Kempers. Tweede bijvak dieroecologie. Dit bijvak, formeel o.l.v. dr. H. Oomen, bestond uit een Master Course in Ecology.
- 1976 - 1977 Master Course in Ecology aan het University College of North-Wales, georganiseerd door prof. P. Greig-Smith. Onder zijn leiding werd deze cursus afgerond met een vergelijking van classificatie- en ordinatietechnieken aan de hand van de vegetatie van Cors Goch, een kalkmoeras. In juni 1979 is het Master Degree verkregen van de University of Wales.
- 1978 - 1980 Aanstelling als wetenschappelijk medewerker bij BION-ZWO op een promotieplaats, toegewezen aan het Instituut voor Oecologisch Onderzoek, standplaats Oostvoorne, binnen het kader van een BION zwaartepunt-project.
- 1981 - heden Aanstelling als wetenschappelijk medewerker aan de Landbouwhogeschool te Wageningen bij de vakgroep Vegetatiekunde, Plantenoecologie en Onkruidkunde.



STELLINGEN

1. Het door Stearns geopperde idee dat een levensstrategie vanwege zijn complexe karakter, een evolutionair star kenmerk zou moeten zijn, vergelijkbaar met complexe morfologische kenmerken en daarom het beste aantoonbaar op hogere taxonomische niveaus, is niet houdbaar.

Stearns, S.C. (1980). Oikos, 35, 266-281.

2. Het ontbreken van aanwijsbare effecten van genetische verschillen tussen populaties van *Plantago lanceolata* L. in kenmerken van de levenscyclus, wanneer deze populaties in elkaars milieu worden overgeplant, verklaren Antonovics en Primack door een grote plasticiteit van deze populaties. Het alternatief, dat de oorspronkelijke milieus niet genoeg en/of niet lang genoeg van elkaar verschilden in relevante kenmerken, is door hen onvoldoende onderzocht.

Antonovics, J. & Primack, R.B. (1982). Journal of Ecology, 70, 55-75.

3. Ten onrechte spreken Warwick en Briggs in hun onderzoek van reciproke transplantatie experimenten. De uitgevoerde proeven laten uitspraken toe over aanpassing aan proefcondities, niet over aanpassing aan veldomstandigheden.

Warwick, S.I. & Briggs, D. (1980a,b,c).

New Phytologist, 85, 275-288, 289-300, 451-460.

4. Het feit dat processen met een sterk historisch en uniek karakter zoals successie en evolutie, een centrale plaats innemen in de oecologie, zou moeten leiden tot een hogere waardering voor vergelijkend en beschrijvend onderzoek.
5. Het ligt niet zonder meer voor de hand vegetaties of zelfs landschappen als objecten voor oecologisch onderzoek te beschouwen. De grens tussen object en milieu wordt in toenemende mate diffuus en dit belemmert de studie van relaties tussen beide.
6. Door de toenemende druk om te publiceren wordt steeds vaker als criterium voor natuurwetenschappelijke betrouwbaarheid gebruik gemaakt van statistische zekerheid in plaats van herhaalbaarheid van de resultaten. Op de lange termijn werkt dit contraproductief.

7. Het systeem van anonieme referenten in het wetenschappelijk bedrijf, is een teken van onvolwassenheid.
8. Voor het idee dat plantesoorten beschermd kunnen worden door een verbod op het plukken van bloemen, bestaan nauwelijks populatie-dynamische argumenten. Een onschuldig en vooral voor kinderen groot plezier aan planten komt hiermee ten onrechte in een kwaad daglicht te staan.
9. Er zijn vele ouders die graag een kind zouden willen adopteren. Er zijn veel kinderen voor wie vergeefs een pleeggezin wordt gezocht. Dit contrast hangt samen met het vaak vertekende beeld dat volwassenen hebben van kinderen.
10. Als het in de strategie theorie ontwikkelde idee juist is, dat een hoge investering in het voortbrengen van nageslacht nu, een negatief effect heeft op het te verwachten aantal nakomelingen in de toekomst, dan valt te vrezen dat de schrijvers van een proefschrift in de toekomst niet al te produktief zullen blijken: zij vertegenwoordigen de strategie van de "big-bang"(re)productie.
11. De kleding die wordt gedragen door de protagonisten tijdens de promotieplechtigheid getuigt wellicht van gevoel voor traditie maar niet van gevoel voor historie: het kan niet de bedoeling zijn weer te geven hoeveel eeuwen de promovendus zijn academische opponenten vooruit is.

*Stellingen, behorend bij het proefschrift van Jan van Groenendael,
Selection for different life histories in Plantago lanceolata.
Heelsum, 16 April 1985.*

druk Casparie Almere