DYNAMICS OF PLANT COMMUNITIES IN FIELD BOUNDARIES

restoration of biodiversity

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Stellingen

1. Het zaadgewicht is een slechte voorspeller van het dispersievermogen van graslandsoorten.

   Dit proefschrift

2. In verstoorde habitats is een stabiel evenwicht mogelijk tussen soorten met kiemrust en soorten zonder kiemrust, ook als deze soorten verder niet in eigenschappen verschillen.

   Dit proefschrift

3. Vooral bij een geringe nutriëntenbeschikbaarheid kunnen de effecten van lage wintertemperaturen op de concurrentie tussen graslandsoorten niet worden veronachtzaamd.

   Dit proefschrift

4. Het verschil in concurrentievermogen van graslandsoorten ten opzichte van elkaar is groter bij een hogere nutriëntenbeschikbaarheid.

   Dit proefschrift

5. Wachten is alleen zinvol als het later beter wordt; vluchten is alleen zinvol als het elders beter is.

   Dit proefschrift

6. Kennis is alleen belangrijk voor wezens die een geheugen hebben en in een werkelijkheid leven waar een verband bestaat tussen verleden en toekomst.
7. Het niet publiceren van statistisch niet-significante onderzoeksresultaten leidt tot veel extra en kostbaar werk.
8. Het maken van Engels tot voertaal in wetenschap en bedrijfsleven is een belangrijk voordeel voor personen die Engels als moedertaal hebben.
9. De overwaardering van slecht nieuws door journalisten bepaalt in belangrijke mate ons wereldbeeld.
10. Gesimuleerde oogsten kunnen de honger niet stillen.

Stellingen behorende bij het proefschrift van Peter Schippers: "Dynamics of plant communities in field boundaries: restoration of biodiversity".
Wageningen, 11 september 2000

Abstract

The field boundary, the strip of semi-natural vegetation bordering arable fields, can be considered an important area for plant species survival in landscapes dominated by agriculture. As the natural plant species diversity in many agricultural landscapes has been reduced in recent decades, the aim of this thesis was to analyse the factors determining biodiversity in field boundaries such as nutrient deposition from the arable field, mowing regime, degree of disturbance and boundary size. For this purpose a simulation model was constructed that comprises the processes and factors that determine the dynamics of the field boundary vegetation. The model was created by integrating three new models: a plant competition model based on eco-physiological principles, a spatially explicit population dynamics model and a seed dispersal model. The models were parameterized and evaluated using experimental data that were partly obtained from experiments described in the thesis. These experiments focused on the plant characteristics determining competition, succession and dispersal. The simulations and experimental results indicated that to enhance the diversity of the field boundary vegetation the following measures should be taken:

1) Preventing nutrient input from the arable field.
2) Mowing and removing of the mown material.
3) Restricting annual disturbance to less than 20% of the area.
4) Keeping the boundary as wide as possible but at least wider than the maximum fertilizer misplacement.

Contents

1

General introduction

Problem definition

The field boundary, the strip of semi-natural vegetation bordering arable fields (see definition Greaves & Marshall 1987), can be considered as an important area for plant species survival in landscapes dominated by agriculture. In recent decades, the natural plant species diversity in many such landscapes has decreased (Boatman 1992, Joenje & Kleijn 1994, Freemark & Boutin 1995). Generally, it is thought, because of the intensification of agriculture (Joenje 1991, De Snoo 1995, Kleijn 1997). Recently, increased environmental concern has caused the ecological value of landscapes by dominated agriculture to become an issue. This thesis, seeks to contribute to the debate on how best to restore the biodiversity of plant communities in agricultural landscapes by looking at the factors and processes determining this biodiversity in grassy field boundaries as generally occur in Dutch agricultural landscapes.

Processes determining diversity

In order to increase diversity in a certain area measures have to be taken that enhance colonization and establishment of new species and/or reduce the local extinction of present species (Figure 1, MacArthur & Wilson 1967). When studying biodiversity change in field boundaries, we have to consider local colonization, establishment and extinction as well as factors affecting these processes.

The probability that new seeds can enter a vegetation depends on the dispersal capacity of the seed and the size and spatial configuration of neighbouring populations. A colonizing seed first becomes part of the soil seed bank (Figure 1). Before this seed can germinate, it has to survive a period in the soil. After germination it has to survive competition from established adults and their offspring to become an established member of the plant community (Schippers 1995). It is for these reasons that successful

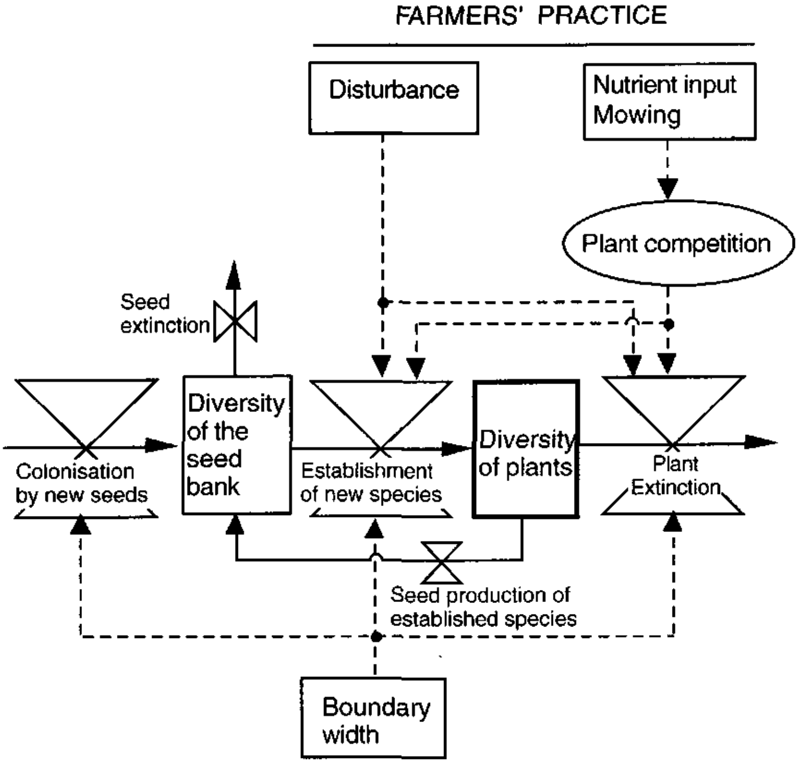

Figure 1. The main relations between farmers' practice, boundary width and plant biodiversity at the landscape level. Dashed lines indicate effects whereas solid lines indicate flow of new or established species numbers.

establishment is generally low and strongly depends on the number of colonized seeds and seedling vigour, which in turn is positively related to the seed mass (Venable & Brown 1988).

Survival of plant species is also affected by interspecific competition (Figure 1). Different plant species may coexist or may exclude each other. Stable coexistence occurs when two plants species grow better as neighbours than when they have own species as a neighbour (Lotka 1932, De Wit 1960). The reason that different plants do better with neighbours of a different species can be found in the theory of niche differentiation, e.g. two species are limited by different nutrients (Tilman 1985) or nutrients are obtained from different soil layers (Berendse 1979).

One species excludes the other when a plant of one species grows better with plants of the other species as a neighbour whereas the other species grows better with plants of its own species as a neighbour. The latter situation is called asymmetric competition (Shipley & Keddy 1994). The level of asymmetric competition determines the rate of exclusion. High asymmetric competition will cause a quick local extinction of the weaker species whereas low competitive asymmetry allows species to coexist for longer.

Other important factors that enhance coexistence are losses that increase with the density of a species. This means that species that are superior in principle are unable to oust other species because at higher densities they are more than proportionally affected by these factors (Huston 1994). Examples of these factors are: diseases, grazing or mowing.

Factors affecting plant biodiversity in field margins

The factors identified as causing the reduction of plant biodiversity in the field boundary are: an increased load of agro-chemicals, an increase of disturbance, changes in mowing regime and a reduction of field boundary area (Joenje 1991, De Snoo 1995, Kleijn 1997).

Agro-chemicals

Four groups of agro-chemicals can be distinguished that may affect field boundary plant species: 1) fertilizers, 2) herbicides, 3) insecticides and 4) fungicides. Although fungicides and insecticides may affect plant diversity, their impact in boundary vegetation is mainly indirect. They reduce the insect and fungi populations which, in turn, may have repercussions on plant populations in the field boundary. Because the effect of these chemicals on the plant population is strongly dependent on the presence, abundance and food-web dynamics of insects or fungi, the study of this system is highly complex and the effect of these agents on plant communities is unpredictable. In this study, I therefore focused on the effect of herbicides and fertilizers which affect plants more directly.

Herbicides may enter the field boundary in two ways: by the direct application of broad-spectrum herbicides to remove weeds in the boundary (De Snoo 1995) and by drift of herbicides from the arable field. Although herbicide drift may affect the vegetation composition of the field boundaries, it has been found that the effects appear to be small compared to those of fertilizer drift (Kleijn & Snoeijing 1997, Kleijn 1997). This thesis therefore concentrates on the effects of broad-spectrum herbicides (which are considered to be a disturbance) and on the effect of fertilizer load on plant diversity in the field boundary.

The deposition of fertilizer in boundaries is inevitable, given the inaccuracy of fertilizer broadcasters (Melman & Van der Linden 1988, Rew et al. 1992). Kleijn & Snoeijing (1997) argued that this load of fertilizer can be regarded as the most important determinant of plant species diversity in field boundary vegetation. With increasing nutrient inputs, they found a strong decrease in species numbers in experimental plots on old arable fields. This indicates that the increase in nutrient availability may lead to an increase in the competitive asymmetry. Intense asymmetric competition induces fast exclusion of species and is therefore an important factor affecting of species diversity (Goldberg & Novoplansky 1997). It has often been suggested that the increase of nutrient availability causes an increase of competitive asymmetry (Grime 1979, Keddy & Shipley 1989, Belcher et al. 1997). Others, however, have stated that competitive asymmetry is not affected by nutrients (Newman 1973, Grubb 1985, Tilman 1988).

The increase of nutrients also leads to an increased biomass. This may reduce the successful establishment of seedlings and could therefore lead to a decrease in biodiversity (Figure 1).

Mowing

Another human impact on field boundary vegetation is mowing. Field boundaries are often mown to prevent the establishment of woody species which may compete for light with the crop. Mowing generally leads to a reduction of competitive asymmetry among plant species, since tall-growing dominant species are affected more than smaller species. Another effect of mowing is that the reduction in height differences reduces competition for light. On average this reduces the difference between species and also the extinction rate of subordinate species. Furthermore, mowing causes a net outflux of nutrients when the mowings are removed from the system. This reduction of nutrient availability in turn causes also a reduction of competitive asymmetry. All these factors may reduce the probability of species extinction.

In a mown vegetation, light can easily penetrate to the soil, enhancing the germination of seeds and the growth of seedlings. If the mown material is removed, mowing causes the litter production to decline which might also enhance establishment because seeds germinate better on soils with a thin litter layer (Berendse 1999). Therefore it can be stated that mowing leads to the establishment of new species. This, plus the fact that mowing also reduces the local extinction of species, confirms the conclusion reached by others (Bakker 1989, Bakker & Olff 1995) that a mowing regime is an important factor determining the plant species diversity .

Disturbance

Disturbance can also be regarded as an important factor determining the plant species composition of a vegetation (Grime 1979). In field boundaries, disturbance can be caused by farming operations with machinery or by the application of broad-spectrum herbicides. Disturbance has two effects on a vegetation: it increases the extinction rate and therefore causes species loss, but it also opens up space for new colonizers from elsewhere, which might lead to an increase of species diversity (Begon et al. 1990) (Figure 1).

Boundary width

Increasing the boundary width will result in an increase of semi-natural area in the landscape. An increase of field boundary area enhances the probability of colonization per boundary length and therefore causes an increase in the number of established species. On the other hand, larger areas can accommodate larger populations having a lower probability of extinction (Schippers 1995). Here, different but interconnected boundary populations may form a meta-population (see Levins 1969). Therefore wide boundaries may support species richness of the boundary vegetation.

Drift of agro-chemicals is inevitable, given that the accuracy of the equipment that distributes these chemicals is generally low (Melman & Van der Linden 1988, Rew et al. 1992, Van de Zande et al. 1995). Therefore wide boundaries may accommodate area that is not affected by the misplacement of agro-chemicals (Melman & Van der Linden 1988, Rew et al. 1992). Since most agro-chemicals (e.g. fertilizer and herbicides) are supposed to adversely affect the biodiversity of the boundary vegetation this shelter function may results in wide boundaries being more diverse.

Objective and approach

To determine the effects of the various factors on the vegetation dynamics in field boundary communities experimentally, a large and long-term experiment should be carried out. An appropriate simulation model, however, could give a quick insight into the effects of the various factors affecting field boundary communities. Another advantage of a modelling approach is that one has to structure knowledge and define processes explicitly. This approach will reveal gaps in knowledge and will identify new topics for future research. We therefore developed a new model (VEGPOP2) comprising the processes and factors that determine the dynamics of the field boundary as described in Figure 1. This main model was the result of the integration of three new simulation models: 1) a plant competition model VEGPOP1, 2) a dispersal model SEEDTRIP and 3) a spatial population dynamics model TRANSPOP. The experiments described in this thesis were conducted to provide parameters for various models and to produce data to evaluate the models.

Although the final model includes processes such as dispersal and establishment, no colonization from elsewhere was included and therefore meta-population processes were not included in this study. The central question this thesis addresses is thus: what are the effects of nitrogen load, artificial disturbance, boundary width and mowing regime on the composition and dynamics of the field boundary vegetation at a local level?

Thesis outline

The central question of the thesis is addressed in Chapter 7. The preceding chapters lead up to this question (Figure 2). Thus, the key question of Chapter 2 is: which plant properties determine whether species are successful in nutrient-rich or nutrient-poor habitats? Then in Chapter 3 a plant competition experiment conducted to explore the role of seasonal change and nutrient availability on the competitive asymmetry between species is described. The eco-physiological assumptions of the final model are evaluated in Chapter 4 using the VEGPOP1 model and the results of the competition experiment of Chapter 3. Data from Chapters 2 and 3 were used to parameterize VEGPOP1.

Chapter 5 examines the role of three life history traits: adult longevity, seed longevity and seed size, in relation to environmental disturbance. In this chapter the TRANSPOP model is described, which spatially simulates the competition between eight population dynamics plant strategies that are permutations of the three traits.

Another model, SEEDTRIP, is described and tested in Chapter 6. SEEDTRIP simulates the process of seed dispersal by wind. Seed shadows

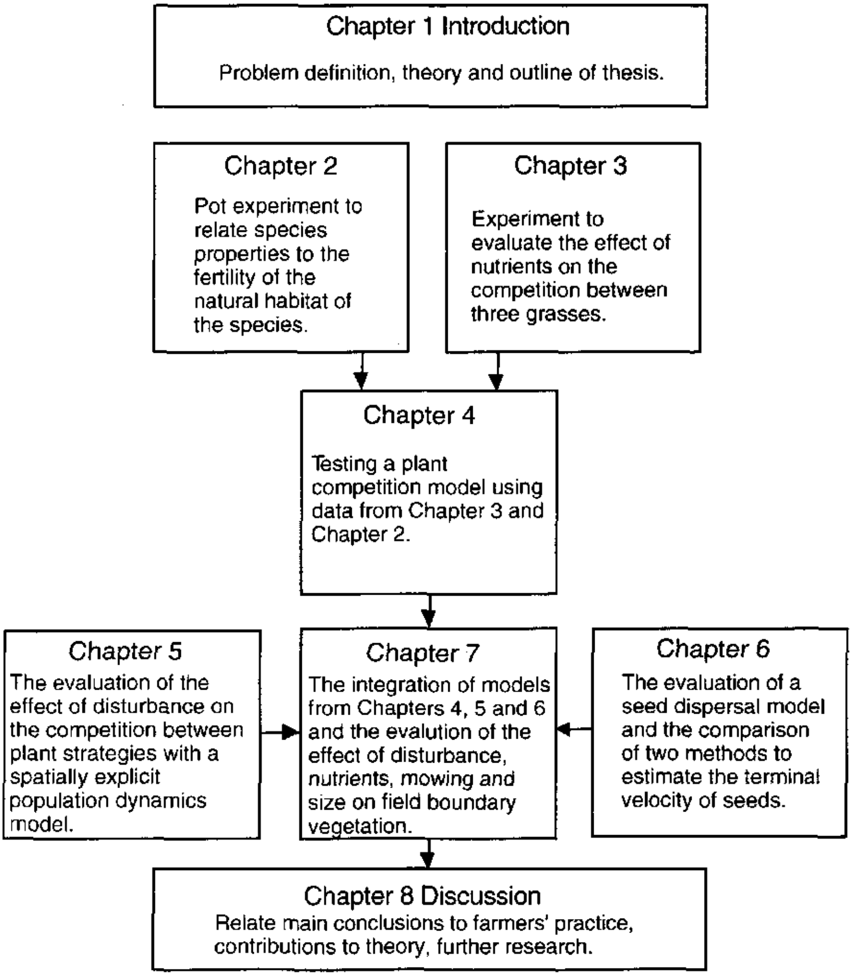

Figure 2. The main flows of information between chapters of this thesis.

generated with this model using actual weather data were used in the final model.

When addressing the central questions in Chapter 7, the VEGPOP1 model was expanded with mineralization, population dynamics (Chapter 5) and dispersal routines (Chapter 6). This final model (VEGPOP2) was used to perform scenario analysis by varying nutrient load, mowing regime, disturbance level and boundary width.

The general discussion (Chapter 8) reviews the main conclusions of this thesis and discusses their implications for farmers' practice and fundamental ecology.

2

Biomass partitioning, architecture and plasticity of eight herbaceous species in relation to their position in an old field succession

Adapted from: P. Schippers & H. Olff (accepted in Plant Ecology)

Abstract

Four grasses (*Poa annua, Holcus lanatus, Anthoxanthum odoratum* and *Festuca ovina*) and four herbs (*Chenopodium album, Rumex obtusifolius, Plantago lanceolata* and *Hieracium pilosella*) were grown in a greenhouse at three nutrient levels in order to evaluate plant allocation, architecture and biomass turnover in relation to successional position.

Four harvests were done at intervals of four weeks. Various plant traits related to biomass partitioning, plant architecture, biomass turnover and performance were determined. Differences in nutrient supply induced a strong functional response in the species shoot-to root allocation, but architecture and turnover showed little or no response. Species from more nutrient-rich successional stages were characterized by a larger specific leaf area and longer specific shoot height (height/shoot biomass), resulting in a faster relative growth rate and total biomass in all nutrient conditions. There was no evidence that species from nutrient-poor environments have superior growth characteristics at low nutrient levels. The only advantage displayed by these species was a lower leaf turnover.

We concluded that species from a nutrient-rich successional stage are specialized in capturing light and nutrients whereas species from a nutrient-poor successional stage are specialized in reducing their biomass and nutrient losses.

Key words: Allocation, biomass turnover, nutrient availability, specific leaf area, specific root length

Introduction

The successional change in plant species dominance depends on the balance between growth and losses of biomass. If the growth of a species exceeds its losses it will increase in biomass. Conversely, if biomass losses exceed growth, the biomass of a species will decrease.

The growth of a species depends on its ability to capture resources such as light and nutrients (Tilman 1985). Biomass senescence, mowing and herbivory determine the loss of nutrients and carbon to the environment. Plants may adapt to nutrient-poor environments either by increasing their ability to compete for nutrients or by reducing losses of nutrients by minimizing their biomass turnover (Berendse & Elberse 1990, Berendse et al. 1992, Berendse 1994).

Various morphological traits determine the ability of species to compete for resources. Light capture in a vegetation is determined by the species height and the distribution of the leaf area over the height (Kropff & Van Laar 1993). In turn, the total leaf area is determined by the specific leaf area (m^2 / g leaf) and the dry weight of the leaves. The height of the plant depends on the specific shoot height (height/g shoot) and the biomass present in the shoot.

Root length is an important determinant to capture nutrients it too can be estimated from the root weight and the specific root length (length/g root). The weight of the different plant parts depends on the biomass partitioning and the total plant weight. So we can distinguish two categories of plant properties: 1) Partitioning, which describes a plant's investment in organs and 2) Architecture, which describes the form of plant parts. Partitioning is ruled by direct trade-offs: biomass investment in a certain plant part cannot be used elsewhere. The plant's architecture is independent on allocation trade-offs and can be considered as a measure of how efficiently biomass is used. A species can make more leaf area and root length with the same amount of biomass by making thinner leaves and roots. But a more efficient plant architecture is often inversely related to tissue longevity (Berendse & Elberse 1990).

Both Tilman (1985, 1988) and Grime (1979) have tried to relate species characteristics to successional sequences. According to the CSR (Competitor - Stress tolerator - Ruderal) framework developed by Grime (1979), species adapted to nutrient-rich environments (such as ruderals and competitive ruderals) are specialized in capturing all resources, below as well as above ground. This means that these species must have high values for their architecture (efficiency). This will result in high relative growth rates (RGR). However, late successional species (stress tolerators) have low values for their architecture and are less efficient in capturing resources but are better at retaining them. Species with the latter strategy specialize in reducing biomass turnover. In this case the major trade-off between species from a nutrient-rich and a nutrient-poor environment is capturing resources versus reducing nutrient losses.

In his resource ratio hypothesis of succession, Tilman (1982, 1985) predicts that plants specialize in capturing the limiting resource. Based upon this theory, we expect that species adapted to nutrient-rich conditions will make major investment in shoots and have high values for shoot architecture because light is the limiting resource in this environment. Species adapted to nutrient-poor conditions are expected to have a low shoot to root ratio and a high specific root length.

The contrasting views of Tilman and Grime have been discussed in various papers (see Thompson 1987, Thompson & Grime 1988, Tilman 1987a,b and Grace 1991) and several experimental approaches have been undertaken in an attempt to relate properties of plant species to their successional position. When sampling plants in the field, Gleeson & Tilman (1990) found that plants growing in late old field successions invested more in roots than in shoots. However, growth chamber experiments gave the opposite result (Olff et al. 1990, Elberse & Berendse 1993, Gleeson & Tilman 1994). Gleeson & Tilman (1994) concluded that these contrasting results still needed to be explained.

Besides that morphological traits sometimes differ between species: traits may vary within a species as a result of plasticity. Plasticity can have two causes: it may be a functional response to environmental change, or to change in the development of a species. Both architectural and allocation properties may be subjected to plasticity, which is why this phenomenon should be considered when species are compared.

To clarify the interaction between allocation, architecture and turnover in relation to the successional position of species we conducted a greenhouse experiment to determine the role of these traits in relation to nutrient availability and successional position. We used the results of this experiment to answer the following questions: 1) Are species that dominate in a certain successional stage specialized in their architecture, allocation and turnover to capture the limiting resource of that stage? and 2) What is the functional response of these traits with respect to nutrients?

Materials and methods

Experimental design

Eight species were selected (Table 1), representing a successional series in a Western European old field succession on sandy soil from a nutrient-rich annual stage to a nutrient-poor perennial stage. To evaluate the species sequence in a more general way we used an ordination of Grime et al. (1988) who classified the species composition of the vegetation in which the species was found (Figure 1).

Three seedlings of each species were planted in 3-liter pots filled with a mixture of 33.3% sandy field soil and 66.6% washed river sand resulting in a sandy soil contained 1.1% carbon and 0.05 % total nitrogen. Ten seedlings per species were measured at the start of the experiment to calculate the initial RGR. The pots were placed according to a random complete block design in 3 blocks in a greenhouse in Wageningen The Netherlands (latitude: 51.58°N, longitude 5.40°E). The initial pot density was 16 pots m^{-2} and decreased to 4 pots m^{-2} at the last harvest. The experiment was started on 28 February 1994. Plants were harvested four times at intervals of 4 weeks.

At the start of the experiment each pot was surrounded by mesh to prevent plant interaction between pots. As a result the area of growth was limited to 298 cm^2. The plants were given NPK fertilizer (15-12-24) at three rates, equivalent to 0, 5, and 20 g of nitrogen m^{-2} (20 g is a regular fertilization rate for pastures in The Netherlands). These treatments will hence forth be referred to as N1, N2 and N3. Throughout the experiment the temperature of the greenhouse was kept above 15 °C and the soil was kept moist to avoid water-limiting growth.

Table 1. Selected species in relation to their successional position after abandonment of old field.

Successional position	Grasses	Forbs
1) Nutrient-rich arable weeds	*Poa annua*	*Chenopodium album*
2) Nutrient-rich perennial stage	*Holcus lanatus*	*Rumex obtusifolius*
3) Intermediate perennial stage	*Anthoxanthum odoratum*	*Plantago lanceolata*
4) Nutrient-poor perennial stage	*Festuca ovina* *ssp. tenuifolia*	*Hieracium pilosella*

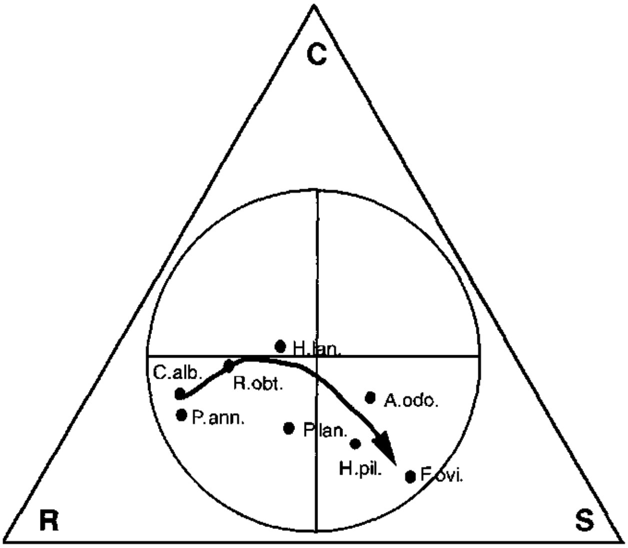

Figure 1. Maximum percentage occurrence of eight selected species according to the triangular ordination of vegetations by Grime et al. 1988. The arrow indicates the direction of an old field succession. Species: P. ann=*Poa annua*, C. alb.=*Chenopodium album*, H.lan.= *Holcus lanatus*, R.obt.=*Rumex obtusifolius*, A.odo.=*Anthoxanthum odoratum*, P.lan.= *Plantago lanceolata*, F. ovi.= *Festuca ovina*, H.pil.= *Hieracium pilosella*, C=competitor, R=ruderal, S=stress tolerator.

Measurements

At each harvest, plants were separated into flowers, stems, living leaves, dead leaves, taproots and roots. The organs were distinguished in a functional way. For instance, a leaf stalk or leaf sheath which has a carrying function were considered as a stem. Leafless flower stalks were classified as flowers. Roots that clearly had a storage function (visual judgement) were considered as taproots (*Rumex obtusifolius* only). These taproots were treated separately in the analysis and were only used to calculate the total biomass production. The dry weight of plant organs was determined after drying at 70°C for two days.

Root length was measured according to the method of Newman (1966). Leaves were harvested in layers of 5 cm and leaf area was measured with an electronic leaf area meter for each layer separately. The measured and calculated parameters are summarized in Table 2. We distinguished four groups of parameters: 1) partitioning parameters indicating where biomass is located at a certain moment, 2) architectural parameters indicating form or efficiency of biomass investment, 3) size related parameters which describe

Table 2. Measured and derived parameters.

Designation	Description
Parameters of partititioning	
FRFL	Dry weight of the flowers and structures to carry flowers divided by TOTBIO (g g^{-1})
FRDLV	Dry weight of dead leaves divided by TOTBIO (g g^{-1})
FRLV	Dry weight of fraction living leaves divided by TOTBIO (g g^{-1})
FRST	Dry matter fraction of morphological structures that carry leaves divided by the TOTBIO (g g^{-1})
FRRES	Fraction of biomass found in the taproot (*R. obtusifolius* only) (g taproot/(TOTBIO+ g taproot)) (g g^{-1})
FRRT	Dry matter of thread-like roots divided by TOTBIO (g g^{-1})
Architectural parameters	
SLA	Specific leaf area (dm^2 leaf/g leaf)
SRL	Specific root length (m wiry root/g wiry root)
SSH	Specific shoot height (height in cm)*(g shoot)$^{-1/3}$
Size related parameters	
HEIGHT	Plant height (cm)
LA	Leaf area of all leaf layers (cm^2/pot)
RTL	Total root length (m/pot)
Parameters of plant performance	
RGR	Relative growth rate between start of the experiment and the first harvest after 4 weeks (week)$^{-1}$
TOTBIO	Total dry matter including dead leaves (without taproots of *Rumex obtusifolius*) (g/pot)
LVMOR	Leaf mortality (g dead leaves)/(g dead leaves + living leaves)

the plant's dimensions and 4) parameters of plant performance which indicate the balance between growth and turnover.

Statistical analysis

Multiple linear regression was performed on partitioning and morphological parameters (Table 3) to search for trends caused by time and nutrient level. This was done for each species separately. As both the annual species matured early, there were no suitable data on these species for the final analysis of the harvest 4 data. Hence factorial analysis of variance was achieved on all parameters of the perennial plant species of harvest 4. Before this analysis the data were transformed (if necessary) according to Steel & Torrie (1981). Means were compared between species of each plant group (grasses or herbs) and within one nitrogen level using Tukey's procedure for pair wise comparison.

Table 3. Partial standardized regression coefficients from a multiple regression analysis calculated individually for each species. Abbreviations according to Table 2.

	Partitioning						Architecture		
Suc.-Sp.	FRFL	FRDLV	FRLV	FRST	FRRT	FRRES	SRL	SLA	SSH
Effect of nutrients									
P. annua	0.122	0.004	0.108	0.732**	-0.688**	.	-0.274	0.245+	0.425**
H. lanatus		0.105	0.272**	0.720**	-0.597**	.	-0.622**	0.054	-0.031
A. odoratum		0.187	0.357**	0.430*	-0.654**	.	-0.119	0.107	0.478*
F. ovina		-0.161	0.637**	0.225	-0.62**	.	-0.369+	0.104	0.271
C. album	-0.029	-0.127	0.055	0.210	-0.462+	.	0.152	0.071	0.043
R. obtus.	.	-.117	0.287**	0.455**	-0.652**	-0.219**	-0.107	0.089	0.607**
P. lanceol.	0.219	-0.075	0.019	0.423**	-0.720**	.	-0.26+	0.153	0.398*
H. pilos.	0.229	-0.136	-0.037	0.440**	-0.611**	.	-0.302+	0.373**	0.203
Effect of time									
P. annua	0.893**	0.915**	-0.940**	0.013	0.415**	.	-0.052	-0.812**	0.290
H. lanatus	.	0.877**	-0.888**	0.094	0.494**	.	0.084	-0.915**	-0.684**
A. odoratum	.	0.635**	-0.834**	0.365+	0.392*	.	-0.428*	-0.910**	-0.321+
F. ovina	.	0.600**	-0.516**	0.044	0.301+	.	-0.482*	-0.776**	0.283
C. album	0.756**	0.734**	-0.857**	0.778**	0.291	.	-0.316	-0.777**	0.662**
R. obtus.	.	0.913**	-0.925**	0.104	0.648**	0.900**	-0.745**	-0.644**	0.593**
P. lanceol.	0.382	0.830**	-0.918**	-0.120	0.326*	.	-0.659**	-0.828**	-0.490**
H. pilos.	0.647**	0.660**	-0.914**	0.687**	0.226	.	-0.525**	-0.812**	0.550**

+=P<0.05, *=P<0.01, **=P<0.001.

Results

Effect of nutrients

In all species, the root fraction decreased when the nutrient supply was increased (Table 3, Figure 2). Conversely the nutrient increase induced an enlargement of both leaf and stem fractions in all species. When the nutrient supply was increased, grasses from a nutrient-rich successional stage and all forbs mainly increased their partitioning to stems, but grasses from a nutrient-poor habitat mainly increased their leaves fraction. The fraction of the biomass in the flowers and dead leaves was not affected by nutrients (Table 3).

The architecture reacted to nutrient supply less strongly than the partitioning (Figure 3). The observed specific root lengths were in agreement with the values found by Noordwijk & Brouwer (1991). In *Holcus, Festuca, Plantago, and Hieracium* the specific root length showed a functional response to the change in nutrients (Table 3). The specific leaf area was relatively insensitive to nutrients; only *Poa* and *Hieracium* showed some increase of this parameter in treatment N3. The increase in nutrients caused an increase of the specific shoot height (SSH in Figure 4) in *Poa, Anthoxanthum, Rumex* and *Plantago* but had no significant effect in the other species.

Effect of time

The leaf fraction generally decreased over time, as the plants invested more in other organs such as roots, flowers, and stems (Table 3, Figure 2). Leaf mortality contributed to this decrease, as it increased over time. *Chenopodium* and *Hieracium* increased their investments in stems during the experiment, but the other species remained at a constant level. With the exception of *Chenopodium* the root fraction in the species from a nutrient-rich successional stage increased during the experiment. Only *Rumex* produced taproots (FRRES) during the experiment. The fraction of the biomass allocated in taproots increased over time. At harvest 4, *Rumex* had allocated 50-70% of the total biomass in its taproots.

Although the species architecture demonstrated low sensitivity for nutrients it changed considerably over time. In most of the cases both SRL and SLA decreased in time. Only in *Holcus* and *Chenopodium* was no significant trend found in the SRL. During the experiment the SSH increased in *Chenopodium, Rumex* and *Hieracium* but decreased in *Holcus, Anthoxanthum* and *Plantago*.

Differences between perennial species

In spite of its large sensitivity for nutrients, root fractions were remarkable similar among the perennial species at the same nutrient treatment (Figure 4, Table 4). However, in treatment N3 in the grass and forb species from a nutrient-poor habitat invested less in the roots. The tested grasses showed a large difference in their shoot investment. In *Festuca,* the decrease of the root investment caused by the increase in nutrient supply favoured leaf growth while in *Holcus* this decrease favoured stem growth. The latter effect caused large differences in leaf fraction in the grasses.

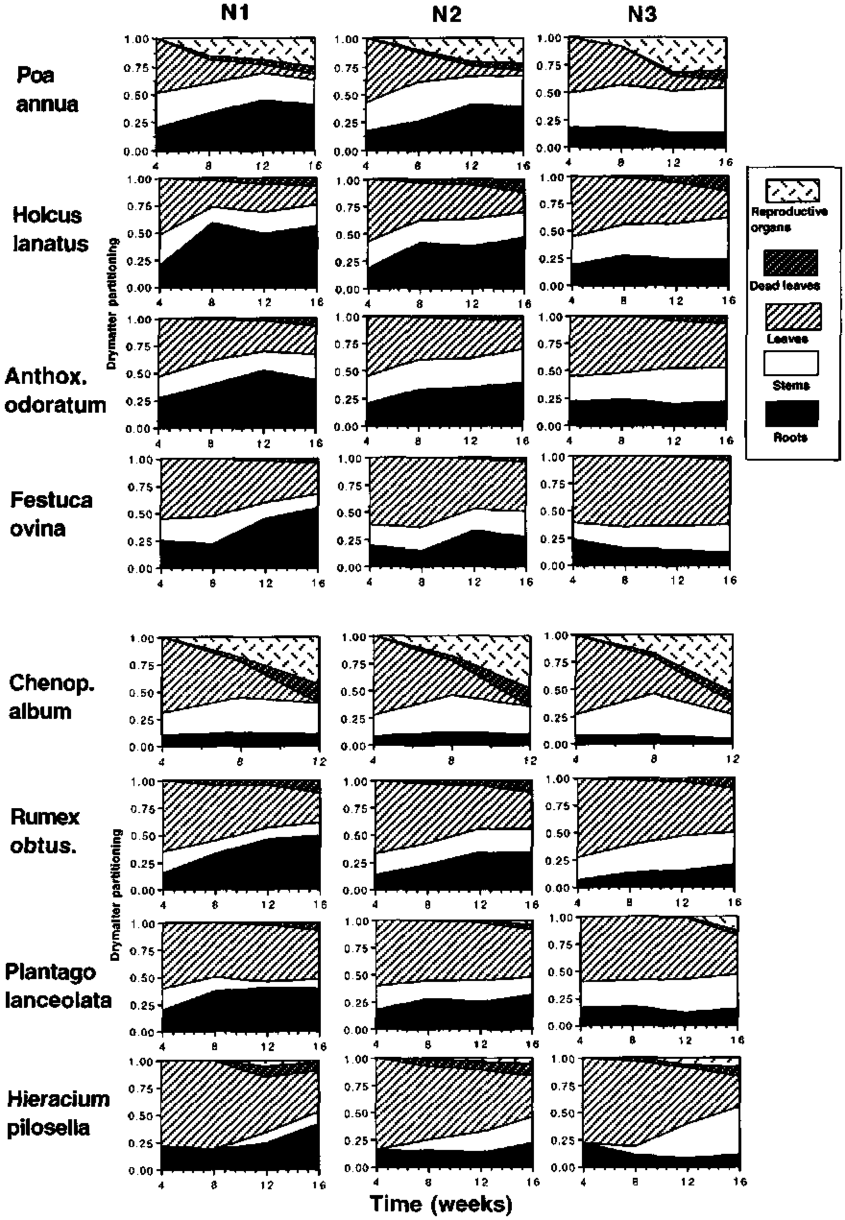

Figure 2. Dry matter partitioning of eight species over time (excluding the taproots of *Rumex obtusifolius*) at 3 nutrient levels N1, N2 and N3 at respectively 0, 5 and 20 g of nitrogen m^{-2}.

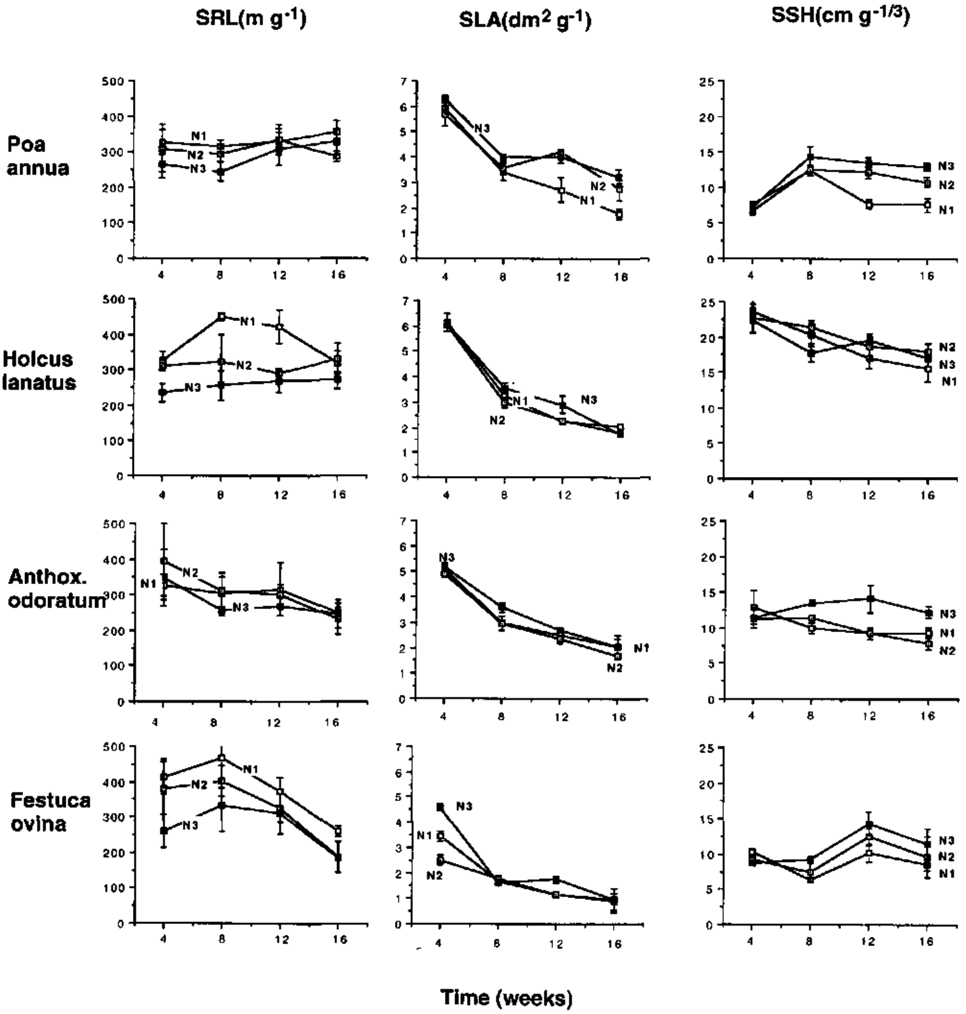

Figure 3a. Temporal development of three important architectural related parameters of four grasses. SRL= specific root length, SLA= specific leaf area, SSH= specific shoot height. N1, N2 and N3 are nutrient applications at respectively to 0, 5 and 20 g of nitrogen m^{-2}.

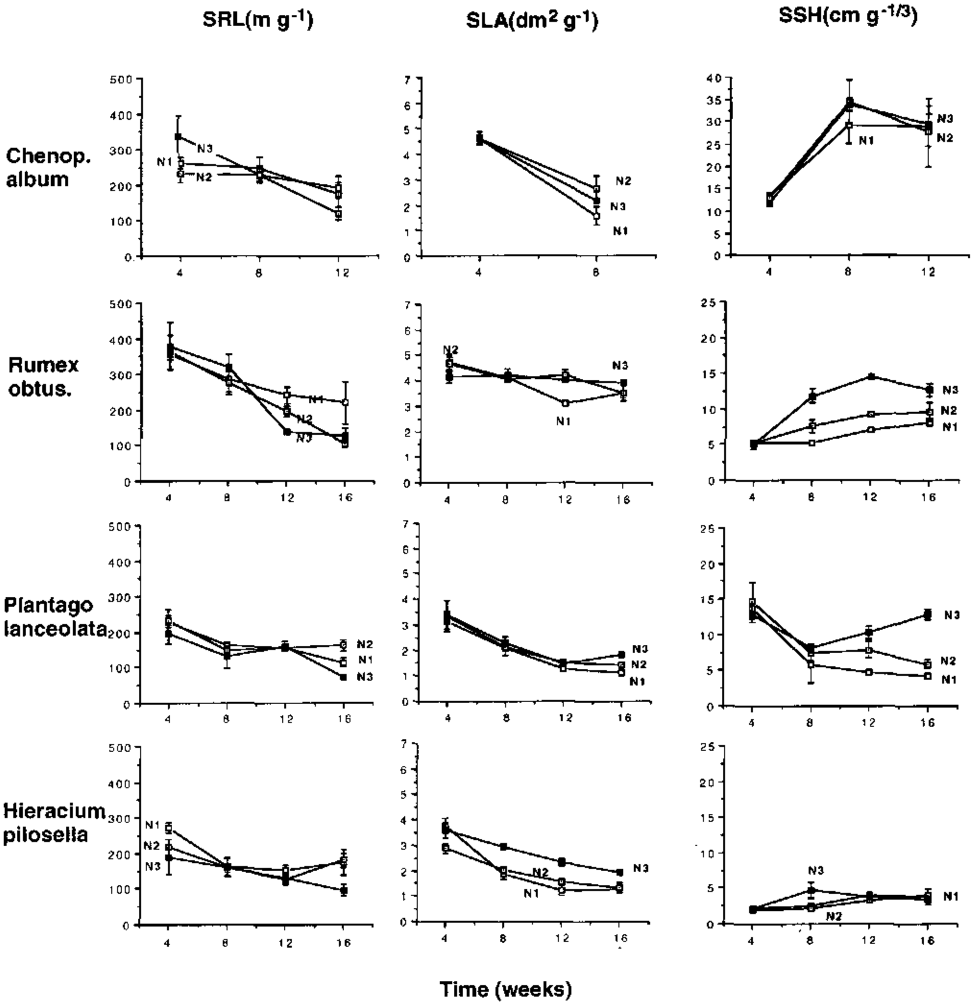

Figure 3b. Temporal development of three important architectural related parameters of 4 herbs. SRL= specific root length, SLA= specific leaf area, SSH= specific shoot height. N1, N2 and N3 are nutrient applications equivalent to 0, 5 and 20 g of nitrogen m^{-2}.

Table 4. F values of a factorial ANOVA on data of the perennial plants after 16 weeks of growth: the effect of species and nutrient application. Abbreviations according to Table 2.

	Grasses			Forbs		
	Sp.	Nutr.	N*P	Sp.	Nutr.	N*P
df	3	3	9	3	3	9
Parameters of partitioning						
FRFL	-	-	-	7.2*	2.5	0.7
FRLV	121.4***	48.7***	5.7*	2.6	0.9	3.4+
FRST	13.1**	25.8***	3.3+	1.3	28.6***	0.6
FRRT	12.1**	66.6***	5.1*	21.2***	121.7***	3.2+
Architectural parameters						
SLA	11.9**	0.3	0.3	231.7***	15.3***	0.427
SRL	7.6*	2.2	0.7	1.8	6.9*	2.9
SSH	19.5***	2.5	0.9	46.2***	12.5**	5.2*
Size related parameters						
HEIGHT	50.1***	33.8***	0.7	84.9***	44.2***	5.1*
LA	44.9***	61.9***	1.0	70.0***	85.4***	1.4
RTL	52.1***	1.0	1.6	14.3**	2.9	3.1
Parameters of plant performance						
RGR[a]	22.2***	3.9+	0.4	63.3***	1.9	0.2
TOTBIO	82.8***	61.0***	-0.8	123.5***	84.1***	1.4
LVMOR	38.6***	0.7	2.4	5.1+	0.0	1.0

+=P<0.05, *=P<0.01, **=P<0.001, ***=P<0.0001

[a] The RGR was calculated over the first 4 weeks of growth and the annual plants were included in this analysis

The specific leaf area (SLA) and the specific shoot height (SSH) were larger in the grass and forb species from a nutrient-rich habitat (Table 4, Figure 5). In the grasses the SRL tended to be higher for *Holcus* in the N1 treatment; no clear trend was found in the forbs. The size-related parameters were, in general, higher in species from a more nutrient-rich successional stage (Figure 6, Table 4). Only in the root length of the herbs there was no clear sequence. The leaf area distribution over the height is graphed in Figure 7, showing the combined effect of nutrient supply and species differences. The perennials of the same successional stage had, in general, a similar leaf area distribution but both annuals differ considerable, *Poa* was much lower than *Chenopodium* which was the highest of all species despite its low biomass

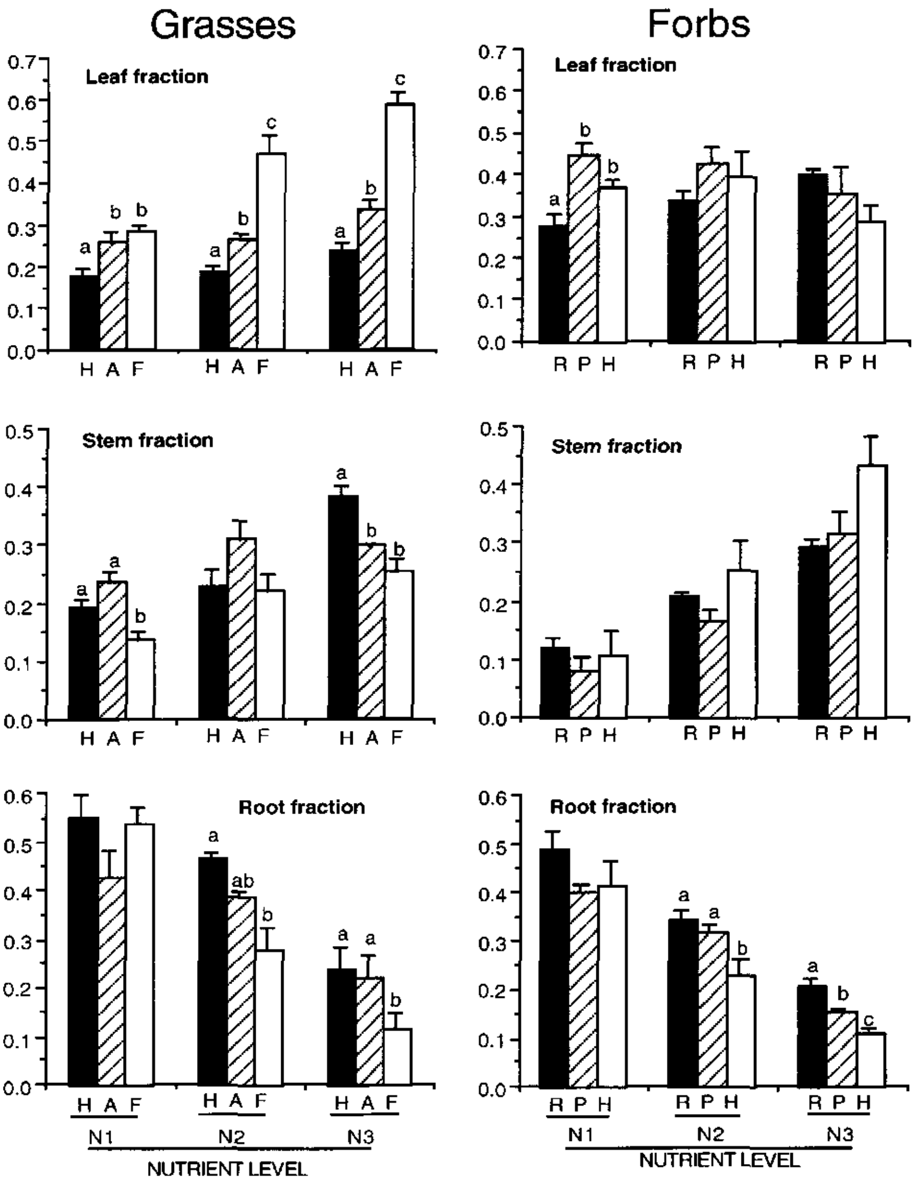

Figure 4. Dry matter fractions of leaves, stems and roots of six perennials after 16 weeks of growth. N1, N2 and N3 are nutrient applications comparable with 0, 5 and 20 g of nitrogen m^{-2}. Grasses: H = *Holcus lanatus*, A = *Anthoxanthum odoratum*, F = *Festuca ovina*. Forbs: R = *Rumex obtusifolius*, P = *Plantago lanceolata*, H = *Hieracium pilosella*. 'a b c' Indicate significant differences (P=0.05) between species within a nutrient level.

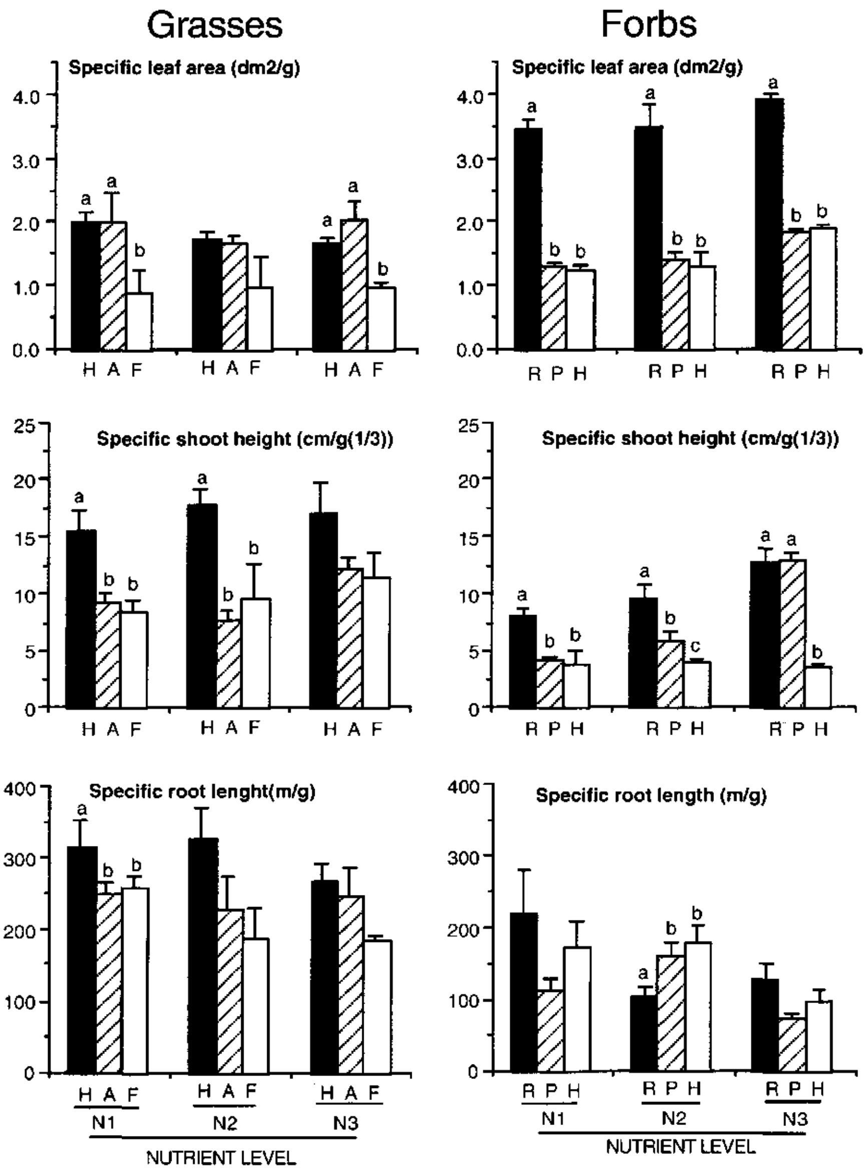

Figure 5. Parameters of plant architecture of the perennial plants after 16 weeks of growth. N1, N2 and N3 are nutrient applications comparable with 0, 5 and 20 g of nitrogen m^{-2}. Grasses: H = *Holcus lanatus*, A = *Anthoxanthum odoratum*, F = *Festuca ovina*. Forbs: R = *Rumex obtusifolius*, P = *Plantago lanceolata*, H = *Hieracium pilosella*. 'a b c' Indicate significant differences (P=0.05) between species within a nutrient level.

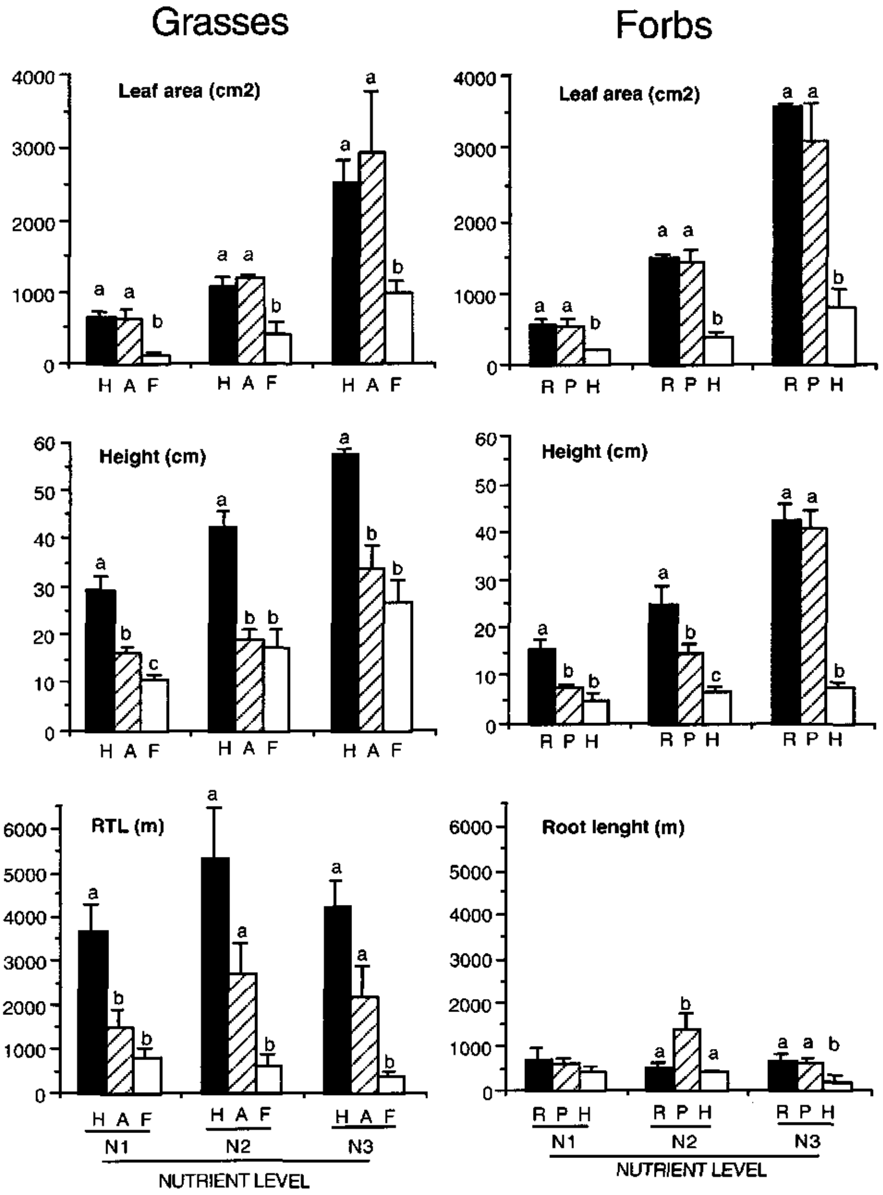

Figure 6. Parameters that represent the plant size of the perennials plants after growing for 16 weeks. N1, N2 and N3 are nutrient applications equivalent to 0, 5 and 20 g of nitrogen m^{-2}. Grasses: H = *Holcus lanatus*, A = *Anthoxanthum odoratum*, F = *Festuca ovina*. Forbs: R = *Rumex obtusifolius*, P = *Plantago lanceolata*, H = *Hieracium pilosella*. 'a b c' indicate significant differences (P=0.05) between species within a nutrient level.

and leaf area. The total biomass at harvest 4 and the RGR, were generally greater in species from a nutrient-rich environment in all nutrient treatments (Figure 8). The pattern of the leaf mortality differed between grasses and forbs. Grass species from a nutrient-poor successional stage had a slower leaf turnover. In the three perennial herbs the leaf turnover differed significantly between the species (Table 4). Figure 7 indicate that *Plantago* and *Hieracium* from a nutrient-poor habitat had also a lower leaf turnover in both N1 and N2 treatment.

Discussion

Method and annual performance

Comparative studies on plant morphology have often been done in short term experiments (Poorter & Remkes 1990, Olff et al. 1990, Olff 1992, Gleeson & Tilman 1994), as these have the advantage of allowing many (small) plants to be tested quickly. In this experiment we monitored eight species over 16 weeks. At the end this time, the productivities were 330, 825 and 1650 g m^{-2} for the N1, N2 and N3 treatments respectively (including dead leaves) which is a realistic productivity range for infertile, moderate fertile and fertile grasslands.

Initially, *Poa* and *Chenopodium,* especially the latter, developed very quickly and were in full flower by week 8. At harvest 3, *Chenopodium* foliage was dead and, at a harvest 4, *Poa*'s foliage was largely dead. This fast development of the annual plants might have been caused by the short day length at the start of the experiment (Warwick & Marriage 1982). Although these species cannot be compared directly with perennial species their architecture and turnover generally fit the pattern of the perennials as discussed below.

Architecture, allocation and turnover

Adapting the theory of Tilman (1985, 1988) we would expect species adapted to nutrient-poor systems to be specialized in capturing nutrients and to have a larger root fraction and a longer specific root length than species from a nutrient-rich environment. The results presented here contradict these expectations, *Festuca* and *Hieracium* (both from a nutrient-poor perennial stage) were found to have the lowest root fraction and within the grasses *Festuca* had the lowest specific root length and in the herbs no trend was found.

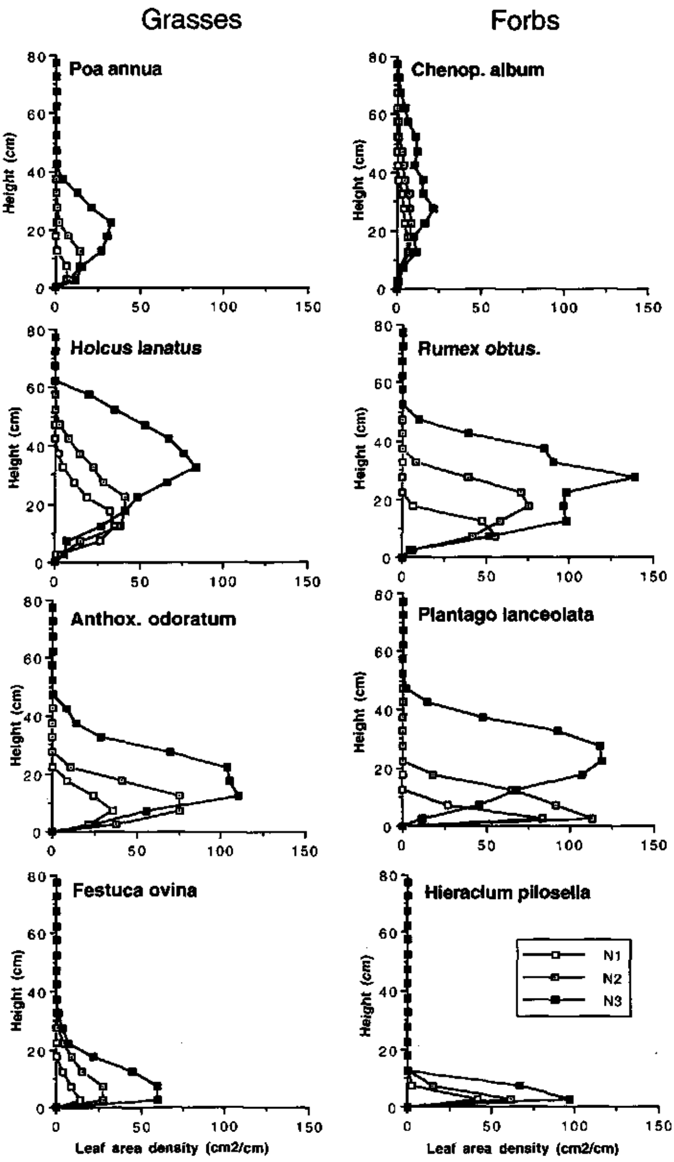

Figure 7. Leaf area distribution over the height of 8 species after growing for 16 weeks (successional order from top to bottom). N1, N2 and N3 are nutrient applications equivalent to 0, 5 and 20 g of nitrogen m^{-2}.

However, contrary to our results, but in accordance to expectations Elberse & Berendse (1993) found higher SRL values in grasses from a nutrient-poor environment. Our experiment would have yielded the same results if a growing period of 4 weeks was considered (Figure 3). However, the SRL of both *Anthoxanthum* and *Festuca* (both from a nutrient-poor habitat) declined over time, whereas the SRL of both *Poa* and *Holcus* remained constant, which resulted in higher values of both latter species at the final harvest. In the experiment conducted by Elberse & Berendse (1993) this trend was mainly generated by high SRL values of two (*Festuca ovina* and *Anthoxanthum odoratum*) out of eight tested species. Furthermore this trend was disappearing at later harvests which might also indicate a decreased SRL of these species in time. This together with our results leads to the conclusion that there is little evidence for the hypothesis that species from a nutrient-poor habitat generally have a longer specific root length.

Light is considered to be the limiting resource in nutrient-rich environments (Tilman 1985) which is why we expected species from a fertile successional stage to have a large shoot fraction and high values for their shoot architecture. The results for the shoot architecture generally confirm these expectations: specific shoot height and specific leaf area were greater in species from a fertile environment. However species, from a nutrient-rich successional stage were found to have a lower or equal shoot fraction which contradicts the expectations.

Compared to Tilman's theory our results fit better in the notions of Grime (1979) who stated that species adapted to a nutrient-rich environment (Ruderals/Competitors) are better in capturing all resources. Compared to the tested species from a nutrient-poor environment these species had a greater specific leaf area, specific shoot height and a longer or equal specific root length and were able to adapt their root investment to a nutrient-poor environment. This means in general that these species are more efficient (size / gram biomass) in increasing their size related parameters such as leaf area, height and root length which enables them to increase nutrient uptake and photosynthesis under all nutrient conditions. Their higher values for the SLA will result in high values for the RGR (Grime & Hunt 1975, Poorter & Reemkes 1990). This brings about a higher biomass, even in nutrient-poor conditions, as shown by our results. On the other hand, Grime (1979) related low RGR to the toleration of nutritive stress. The mechanism enabling these slow-growing plants to perform better at low nutrient levels has to do with

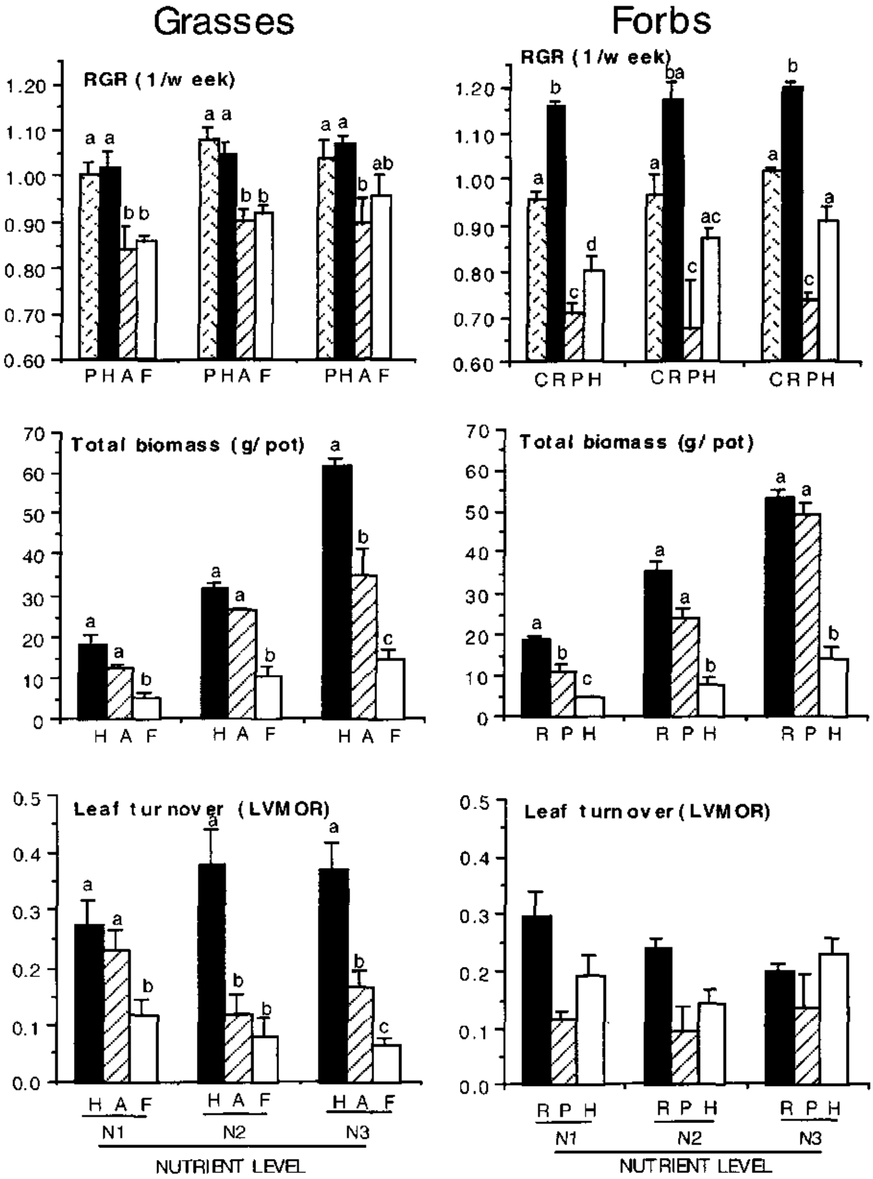

Figure 8. An overview of the RGR (first 4 weeks), the total biomass (after 16 weeks) and leaf mortality (after 16 weeks) related to the successional order of the species. N1, N2 and N3 are nutrient applications equivalent to 0, 5 and 20 g of nitrogen m^{-2}. Grasses: H = *Holcus lanatus*, A = *Anthoxanthum odoratum*, F = *Festuca ovina*. Forbs: R = *Rumex obtusifolius*, P = *Plantago lanceolata*, H = *Hieracium pilosella*. 'a b c' indicate significant differences (P=0.05) between species within a nutrient level.

their lower biomass turnover. Our results show that the dead leaf fraction in grasses adapted to nutrient-poor environments was indeed lower than in the grasses adapted to nutrient-rich environment. In the herbs, no such trend was found, but at a low nutrient availability both *Hieracium* and *Plantago* had a lower leaf turnover than *Rumex*. This may indicate that the mortality rate of the grass and herb species adapted to nutrient-poor conditions is lower. The low biomass turnover has two important consequences: 1) it will result in a higher biomass in the long term (Schläpfer & Ryser 1996), and 2) species with a low turnover will lose less nutrients to the environment (Berendse & Elberse 1990). This results in a more efficient nutrient economy and relatively high biomass, enabling the species in question to compete successfully in a nutrient-poor environment (Aerts 1995).

The above section raises the question of why there are no species with high values for architecture and with a low biomass turnover that will be superior competitors in all environments. In other words: why is there a inverse correlation between architectural parameters and biomass turnover? The answer may be found in the relation between architecture and tissue density. High values for architecture, which are expressed in (fresh) size / gram dry weight, are negatively related to tissue density expressed in dry weight / fresh weight (Poorter & Bergkotte 1992). This low tissue density may be the cause of the short longevity, since this density can be regarded as an indicator of the longevity of the plant's tissue (Ryser & Notz 1996).

Plasticity

Allocation was found to be more sensitive than architecture to the nutrient level. No evidence was found for any plasticity in the architecture of grasses but in the herbs there were major changes in the specific shoot height of *Plantago* and *Rumex* in response to the nutrient level. This effect was caused by a change in leaf angle of these rosette species. Plants growing in treatment N3 had more vertical leaves which resulted in taller plants while in treatment N1 the leaves and stems of both species had a more horizontal orientation. This effect was also reported by Olff (1992).

It was the plasticity of the shoot-to-root allocation that was largely responsible for the change in dry matter partitioning at different nutrient levels. This effect was noticed over 30 years ago by Brouwer (1962). With the increase of nutrient availability the herbs invested more in stems at the expense of roots, while grasses invested in both leaves and stems. The difference in root allocation between the species in the N3 treatment was striking. In these condition, species from a fertile environment invested relatively more in their roots than species from a nutrient-poor environment. A possible reason for this effect might be the higher relative growth rate of these species. Because they grew faster they needed more nutrients, and may have depleted the soil bringing about a functional response in the shoot-to-root ratio. This effect might also explain the results of Olff et al. (1990), Elberse & Berendse (1993) and Gleeson & Tilman (1994) who also found lower shoot-to-root ratios in species adapted to a nutrient-rich environment. If we include this depletion effect, the functional response of the root fraction of the perennials tested can be regarded as similar between the species. This similar functional response of the root allocation may support the hypothesis that species are able to optimize their shoot-to-root allocation to optimize the growth rate at different nutritive conditions (Levin et al. 1989, Van der Werf et al. 1993, Gedroc et al. 1996).

Conclusions

In this research, we examined biomass allocation, architecture and plasticity of species from different successional stages of an old field succession and found that the availability of nutrients primarily affected the shoot-to-root ratio of the species but had a limited effect on the plant architecture. Our results indicate that species from a nutrient-rich successional stage generally have a larger specific leaf area and higher specific shoot height. This makes these species more efficient growers and competitors because the larger specific leaf area causes a faster RGR, and the higher specific shoot height causes taller plants which makes these species better competitors for light. We did not find that species from a nutrient-poor successional stage to have a superior architecture or allocation to compete for nutrients nor did we find evidence for any compensating growth-related properties in which they were superior to species from a nutrient-rich successional stage. The only advantage later successional species have was a lower biomass turnover. This may have a significant effect on the biomass and nutrient loss in the long run. Our final conclusion is therefore that species from a fertile environment are growth oriented and are specialized in the capture of light and nutrients, whereas species from an infertile environment are specialized in reducing their biomass and nutrient losses.

3

Competition under high and low nutrient levels among three grassland species occupying different positions in a successional sequence

Adapted from: P. Schippers, I. Snoeijing & M. J. Kropff (1999) New Phytologist 143: 547-559.

Abstract

To clarify the role of seasonal change, competitive response and nutrient availability in the competitive asymmetry of grassland species a competition experiment was conducted on *Holcus lanatus* L., *Anthoxanthum odoratum* L. and *Festuca ovina* L. which represent a successional sequence of decreasing nutrient availability. Seven harvests were taken over two growing seasons. At each harvest the dry weight of plant parts, dead leaves, leaf area and plant height were measured. Three key traits, that determine the successional status of the species were studied: specific leaf area (SLA), specific shoot height (SSH), and dead leaf fraction.

The response of these traits to competition appeared to be limited and insufficient to change the competitive relations in the experiment. However, all three traits showed marked seasonal changes, which resulted in superior growth and survival in winter of the species adapted to nutrient-poor environments. The findings support the theory that competitive asymmetry increases at higher nutrient levels. It is postulated that the directionality of light makes it possible for the dominant species to monopolize this resource more easily than nutrients.

Key words: Biomass turnover, competitive asymmetry, competitive response, seasonal change, specific leaf area, specific shoot height, succession

Introduction

One of the most important determinants of species composition in grasslands is the availability of nutrients: it determines the competitive balance between fast- and slow-growing species (Grime 1979). Species with high relative growth rates (RGR) dominate on fertile soils, whereas species with a low RGR dominate on infertile soils (Grime & Hunt 1975).

The two most important morphological characteristics of nutrient rich grassland species are a high specific leaf area (SLA) which is responsible for the high RGR (Poorter & Remkes 1990, Poorter & Lambers 1991, Hunt & Cornelissen 1997) and a relatively tall plant architecture (Grime 1979, Elberse & Berendse 1993). The tall architecture can be described by the Specific Shoot Height (SSH cm height·g shoot$^{-1/3}$). Both SLA and SSH can be considered as characteristics that make species superior competitors for light (Tilman 1985). Surprisingly, species adapted to nutrient-poor environments are not better at capturing nutrients: they do not invest more in their roots (Olff et al. 1990, Elberse & Berendse 1993, Van de Vijver et al. 1993, Gleeson & Tilman 1994), nor do they not have generally longer specific root length (SRL) (Ryser & Lambers 1995) or more root absorption capacity (Chapin 1980). Although there is some evidence that slow growing species can respond proportionally more to nutrient patches and pulses (Robinson & Van Vuuren 1998), the key characteristic of species from nutrient-poor environments is their lower biomass turnover (Berendse et al. 1987, Aerts et al. 1990, Schläpfer & Ryser 1996) which is responsible for a more efficient nutrient economy (Berendse & Elberse 1990). Thus, it can be stated that species adapted to nutrient-rich environments are characterized by a high SSH and SLA, whereas species adapted to nutrient-poor habitats are characterized by low biomass turnover.

According to the definition of Shipley & Keddy (1994), asymmetrical competition occurs when one species (the dominant) experiences less intense interspecific competition than intraspecific interaction while the other species (the subordinate) experiences more intense interspecific interaction than intraspecific interaction. Intense asymmetric competition results in rapid exclusion of species and is therefore an important determinant of species diversity (Goldberg & Novoplansky 1997). Two contrasting hypotheses have been put forward to describe the relation between nutrient availability and competitive asymmetry: one predicts that competitive asymmetry is independent of the availability of nutrients (Newman 1973, Grubb 1985, Tilman 1988) and the other presumes that competitive intensity increases with nutrient availability (Grime 1979, Keddy 1989). Both hypotheses are supported by experimental evidence. Wilson & Tilman (1991) and Turkington et al. (1993) reported no effect of nutrients on the level of competitive asymmetry whereas others found that competitive asymmetry increases with the nutrient availability (Belcher et al. 1995, Keddy, at al. 1997). These contrasting views indicate a need for more evidence on this topic.

The competitive ability of individual plants can be compared between species in two distinct ways: in terms of the *competitive effect* or ability to suppress other individuals and in the *competitive response* or ability to avoid being suppressed (Goldberg & Landa 1991). Our understanding of competition between plants is hampered by the competitive response to overtopping by other species. The two important architectural traits (SLA, SSH) respond in a functional way to the availability and quality of light (Rice & Bazzaz 1989, Olff 1992, De Kroon & Knops 1990, Kropff & Van Laar 1993). If both increase, the plant is better able to compete for light. This functional response may reduce the competitive effect of the overtopping species and hence the competitive asymmetry between the species.

Most competition experiments on perennial species have lasted for only one growing season (Berendse et al. 1992, Keddy at al. 1997, Schenk et al. 1997). But by excluding the winter period and regrowth in spring an important period in mowed agricultural and semi-natural grasslands is excluded. For instance, the important characteristics SLA, SSH and biomass turnover may be temperature-dependent and might change during the season. Furthermore the reduced availability of light in winter might alter the competitive ability of species. For these reasons a competition experiment that monitors these important characteristics for longer than one year might elucidate the effect of seasonal change on interspecies competition.

Our competition experiment with harvests covering two growing seasons was aimed at clarifying the role of seasonal change, competitive response and the effect of nutrients on the competitive asymmetry of grassland species. Three species were selected to represent a successional sequence with respect to nutrients based upon ecological characterization made by Grime at al. (1988). *Holcus lanatus* L. was chosen to represent species of nutrient rich environments and *Festuca ovina* L. ssp. *tenuifolia*

(Sibth.) represented species of nutrient-poor environments; *Anthoxanthum odoratum* L. was considered to be representative of species thriving at intermediate nutrient levels. We used the results of the competition experiment to answer three questions: (1) What is the effect of competitive response of the important traits SLA, SSH and biomass turnover on the competition between the species? (2) Does the competitive asymmetry or intensity increase with the nutrient availability in the species studied or is it independent of nutrient availability? (3) Is the competitive ability of species affected by seasonal change?

Materials and methods

Experimental design

The experiments were conducted in an unheated roofed glasshouse (50% open at the sides) in Wageningen, The Netherlands (51.58° N, 5.40° E) from 1 June 1995 until 1 October 1996. The average daily temperature in the glasshouse during the experimental period was about 3.4 °C higher than the outside temperature and the radiation intensity was 74% of that outside. The seasonal pattern of temperature and radiation in the glass house is shown in Figures 1 c,d.

Seedlings of similar dry weight (*Holcus* = 0.57 mg, *Anthoxanthum* = 0.51 mg, *Festuca* = 0.36 mg) were planted in square 3-litre pots (surface area= 256 cm^2) containing 1/3 sandy soil and 1/3 clean sand. This potting soil had a total C content of 0.4 % and a C/N ratio of 20. Seven competition treatments were established (according to the replacement design of De Wit 1960) by planting various combinations of species: three monoculture treatments with one species per pot (six seedlings of one species); three mixed treatments with two species per pot (three seedlings of each species); and one mixed treatment with three species per pot (two seedlings of each species). Two nutrient levels were established, called N0 and N20. In the N20 treatment, 3.14 g NPK fertilizer (15% nitrogen, 12% phosphorus and 24% potassium) was applied (Table 1), which was equivalent to a rate of 20 g of nitrogen m^{-2}. No fertilizer was applied to the N0 treatment. Nitrogen mineralization of the soil was measured *in situ* during the experiment (Raison et al. 1987). Soil samples were collected each harvest and available nitrogen was extracted with 0.01M $CaCl_2$ (Houba et al. 1986). The total N mineralization throughout the experimental period was 3.8 g N m^{-2} in both nutrient treatments. The seasonal change in mineralization is shown in Figures 1a, b.

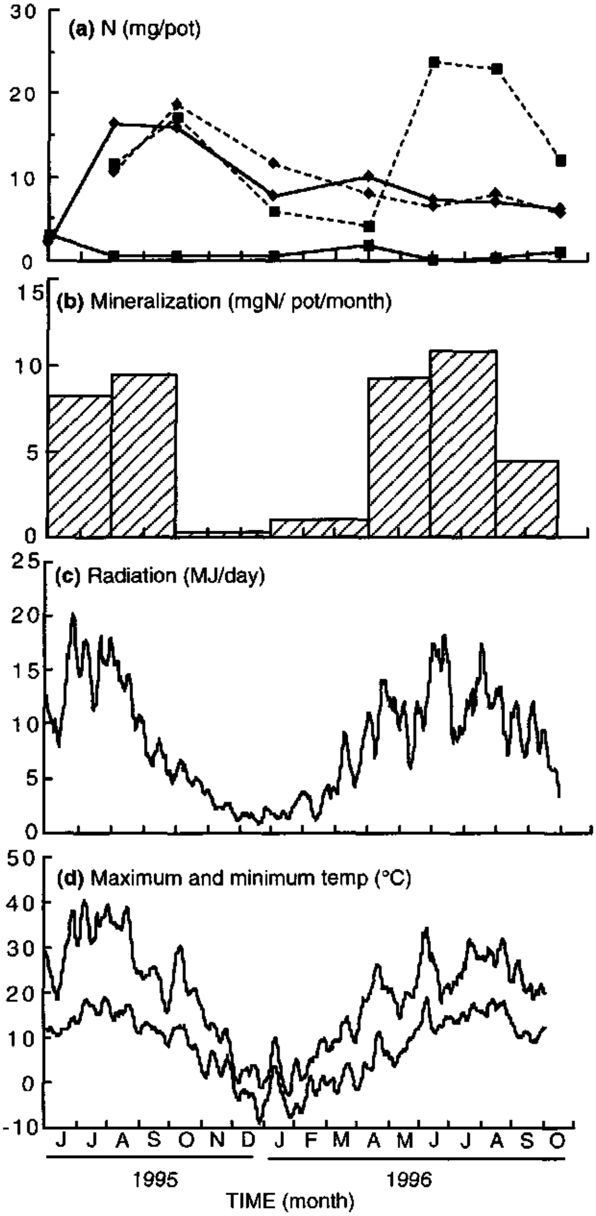

Figure 1. (a) Measured values of nitrate-N (——■——), incubated values of nitrate-N (---■--), measured values of ammonium-N (——◆——), incubated values of ammonium-N (---◆--- dotted line), incubated values are measured in incubation tubes (2 or 3 months incubation) without uptake by plant (b) total N mineralization, (c) radiation and (d) temperature in the greenhouse during the experimental period. Every point of the line in graph (c) and (d) represents a weekly mean.

Seven pots from the same competition treatment (one per sampling date) were placed together to form a plot with a density of 234 plants m^{-2}. To minimize edge effects, each plot was surrounded by green netting material with a light transmission of 10% kept 10 cm below the top of the canopy. The plots were arranged in a random complete block design with 4 replicates. The soil in the plots was kept at field capacity during the experiment, to ensure that growth was not limited by shortage of water. To represent a grassland situation, where plants are mown at least annually, all plants were clipped in October at the second harvest to a height of 3 cm. The timing of events is given in Table 1.

Table 1. Schedule of events. All events happened in the first week of the named month.

Date	Events
June 1995	Start of experiment
July 1995	NPK application (N20)
August 1995	Harvest 1
October 1995	Harvest 2 and mowing
January 1996	Harvest 3
April 1996	Harvest 4
June 1996	Harvest 5
July 1996	NPK application (N20)
August 1996	Harvest 6
October 1996	Harvest 7

Measurements

Plants were sampled bi-monthly, except during winter, when the interval was 3 months (Table 1). At each sampling time, one pot of each plot was harvested (4 replicates per treatment). Shoot height and dry matter of reproductive organs, leaves, dead leaves and stems were measured. Root dry matter was measured only in the monoculture treatments. The living stem weight (W_{st}) was calculated by adding the weight of living stubble (stems below 3 cm) to the weight of living stems above 3 cm. The amount of living stubble, in turn, was estimated by multiplying the proportion of living tillers by the stubble weight. Before weighing, plant samples were dried in an oven at 70 °C for two days. Table 2 shows the plant characteristics calculated from the measured data.

Table 2. Measured and calculated variables.

Designation	Description
measured	
IW	Weight of seedling at planting (g)
W_{fl}	Dry matter of reproductive organs (g/pot)
W_{lv}	Dry matter of living leaves (g/pot)
W_{dlv}	Dry matter of dead leaves (g/pot)
W_{st}	Dry matter of stems (g/pot)
W_{rt}	Dry matter of roots (g/pot) (monocultures only)
Height	Total plant height (cm)
LA	Total leaf area (cm^2)
calculated	
W_{tot}	$W_{rt}+W_{st}+W_{lv}+W_{fl}$ (g/pot)
RGR*	$(\ln(W_{tot})-\ln(IW))/60$ (d^{-1})
W_{sh}	$W_{lv}+W_{st}$ (g/pot)
SLA	$LA/(W_{lv}*100)$ (dm^2 g^{-1})
SSH	Height * $W_{SH}^{-1/3}$ (cm g$^{-1/3}$)
F_{dlv}	$W_{dlv}/(W_{lv}+W_{dlv})$
RY	Relative Yield: W_{sh} Mixture / W_{sh} Mono

* W_{tot} measured at harvest 1, 60 = number of days between planting and first harvest.

Total leaf area of *Anthoxanthum* and *Holcus* was measured with a Li-cor electronic area meter (MODEL 3100). This equipment was however not sensitive enough to measure the fine *Festuca* leaves for which a portable leaf area meter (Li-cor model 3000) was used.

Analysis of data

Since the turnover of shoots and roots is considered to be correlated (Schläpfer & Ryser 1997) the dead leaf fraction (F_{dlv}) was chosen as the variable characterizing biomass turnover. The RGR was estimated based upon the seedling growth from the start of the experiment until the first harvest Table 2). Further the relative yield (RY) was calculated as the shoot weight (W_{sh}) in the mixed culture, divided by the shoot weight in monoculture (Table 2). The specific shoot height (SSH) was calculated as the ratio between the height and the third order root of the shoot biomass. The third order root was taken because the shoot biomass is more related to the occupied space of a plant (volume) than to the height (Yoda et al. 1963). The value of the SSH is therefore independent of the plant weight when plants grow isomorphically and when the occupied space per gram biomass is constant.

Analysis of variance was used to search for differences between species , the effect of nutrients and competitive response. If necessary, the data were log transformed to homogenize the variance (for criteria see Sokal & Rohlf 1995).

Results

Species in monoculture

The RGR over the first growing period was faster in the nutrient-rich treatment in all species (Figure 2 Table 3). Furthermore, at both levels of nutrition, the RGR was faster in the species adapted to a nutrient-rich environment. The differences in RGR in both nutrient conditions resulted in *Holcus* initially performing better than *Anthoxanthum,* which performed

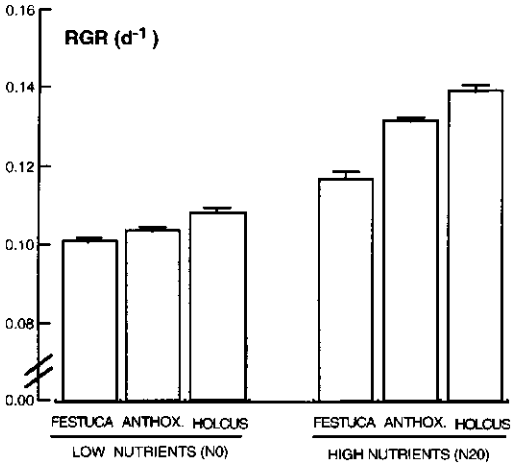

Figure 2. RGR values (total plant) of the species growing in monoculture under two nutrient conditions: N0 no nutrients were applied, N20 high nutrient treatment, comparable with 20 g of N m^{-2}. Error bars indicate ±1 SE (n=4).

Table 3. F values of the analysis of variance of the monoculture data (time is not shown). Plant characters designated according to Table 2.

character	species	nutrients	sp*nut
df	2	1	2
RGR	69.3***	1458.5***	18.4***
W_{tot}	15.8***	1971.4***	11.4**
F_{dlv}	381.6***	0.7	0.9
SLA	894.8***	51.1***	3.4
SSH	28.4***	0.0	1.3

+=P<0.05, *=P<0.01, **=P<0.001, ***P<0.0001; error df = 123

better than *Festuca* (Figure 3). In the N0 treatment, however, (October 1996) this sequence had changed after two growing seasons (Figures 3 a,c,e): *Festuca* then had the most biomass, *Holcus* was second and *Anthoxanthum* the least. In the high nutrient treatment, *Holcus* had the most biomass at the end of the experiment while *Anthoxanthum* had the least. The addition of nutrients increased total biomass by a factor of about 8 in all species.

Mowing decreased above-ground biomass after 1 October 1995 and affected taller species like *Holcus* and *Anthoxanthum* more than *Festuca*. In the N0 treatment *Holcus* lost 61% of the above-ground biomass compared with 55% for *Anthoxanthum* and for *Festuca* 47%. These values were higher under high nutrient conditions: 82% for *Holcus*, 79% for *Anthoxanthum* and 61% for *Festuca*. The natural mortality, indicated by the dead leaf fraction (F_{dlv}), differed considerably between the species (Figure 3, Table 3). *Festuca* had a lower turnover than both other species. This variable was not affected significantly by nutrient supply.

The SLA was significantly different between the species (Figure 4, Table 3) because *Festuca* differed greatly from the two other species. The application of nutrients generally increased SLA. The SLA showed seasonal change, being lower in winter. *Festuca* had also a much lower SSH in monoculture than either of the other species (Figure 5). However, this trait was not affected by the nutrient availability.

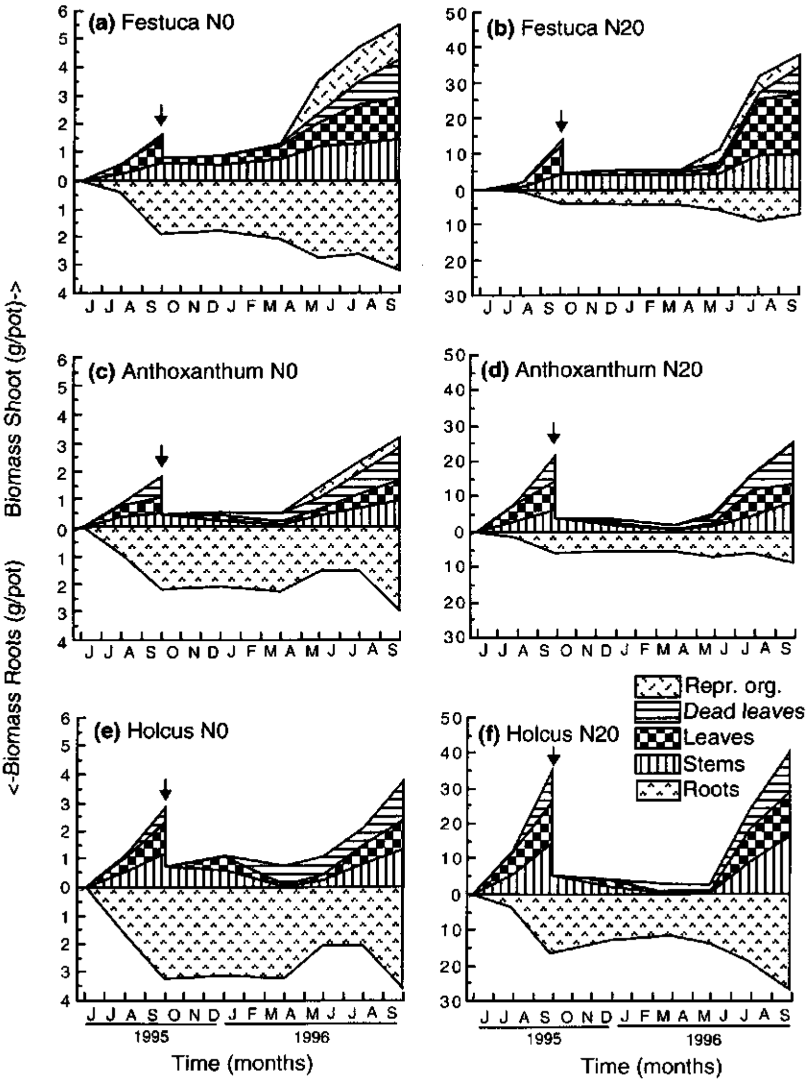

Figure 3. Biomass of shoot and root over two growing seasons in monoculture, categorized by plant parts. The arrow indicates the time when the vegetation was cut. N0 low nutrient treatment with no fertilizer addition; N20 nutrient-rich condition with a fertilizer application of 20 g N m^{-2}.

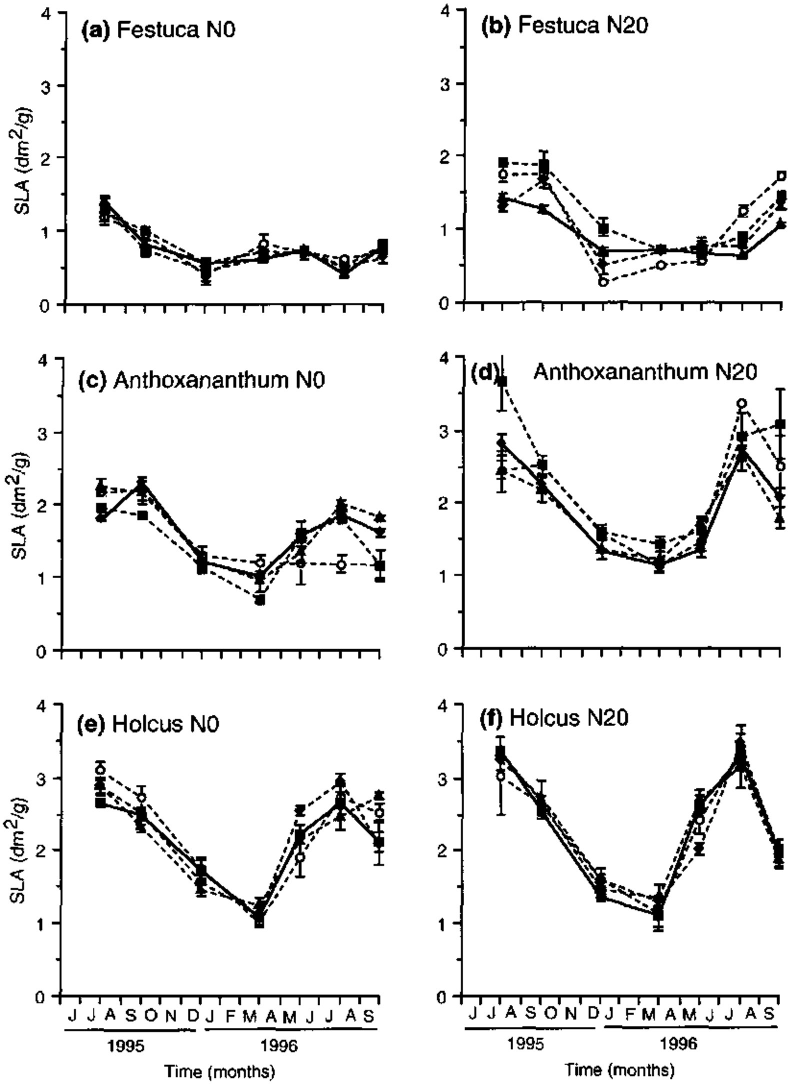

Figure 4. Specific Leaf Area (SLA) of the three grass species over two growing seasons. Each graph depicts 4 lines of the same species in different competitive treatments. (———) = SLA in monoculture; (-------) = SLA in competition; (■) = *Holcus lanatus* as competitor; (◆) = *Anthoxanthum odoratum*, as competitor; (▲) = *Festuca ovina* as competitor; (○) = competition with both other species. Error bars indicate ± 1 SE (n=4). N0 no nutrients were applied; N20 high nutrient treatment comparable with 20 g of N per m^2.

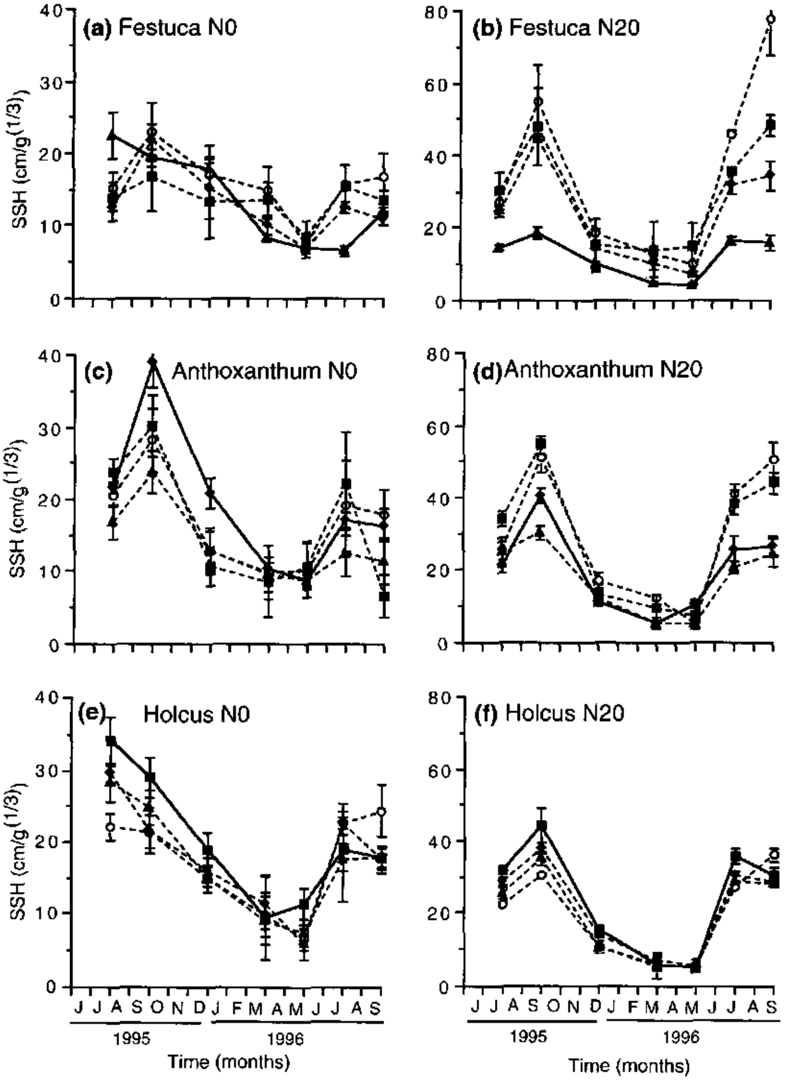

Figure 5. Specific Shoot Height (SSH) of the three grass species over two growing seasons. Each graph depicts 4 lines of the same species in different competitive treatments. (———) = SLA in monoculture; (-------) = SLA in competition; (■) = *Holcus lanatus* as competitor; (◆)= *Anthoxanthum odoratum*, as competitor; (▲) = *Festuca ovina* as competitor; (○) = competition with both other species. Error bars indicate ± 1 SE (n=4). N0 no nutrients were applied; N20 high nutrient treatment comparable with 20 g of N per m^2.

Species in mixture

Figure 6 depicts the results of plant performance expressed as shoot weight (W_{sh}) in the mixed treatments. In the first season, *Holcus* did better than *Anthoxanthum*, while *Anthoxanthum* did better than *Festuca* in the N0 treatment (Figures 6 a-d). In the second season, however, *Festuca* was able to take over the second position from *Anthoxanthum* and the differences between *Holcus* and *Festuca* diminished. This change in performance started in early spring. The RGR of the shoot between 1 March and 1 April can be considered as a good indicator for the regrowth capacity of the species in spring. In the N0 treatment, where all species were present, the RGR values were 0.037 (d^{-1}) for *Festuca*, 0.020 for *Holcus* and 0.007 for *Anthoxanthum* which indicates the good performance of *Festuca* in this low nutrient treatment.

In the N20 treatment *Holcus* was able to suppress nearly all growth of its antagonists (Figures 6 e-h). *Anthoxanthum* was a better competitor in this high nutrient situation than *Festuca*, as can be seen from its better performance in competition with *Holcus* compared with *Festuca* and by its superior growth when grown together with *Festuca*

The relative yield (RY) indicates how plants in mixtures performed compared with plants in the monoculture (Figure 7). The 0.5 line in two species mixtures and the 0.33 line in the three species mixture indicate the equal performance line (performance of mixed culture = performance monoculture). For instance *Holcus* was always performing above this equal performance line indicating that it was more suppressed by other *Holcus* plants than by the presence of *Festuca* or *Anthoxanthum* plants (Figures 7 a-d, e-h). In general, the RY graphs show the same pattern as the biomass graphs, except that the RY differences are smaller; from this we infer that the dynamics of the shoot (WSH) in the mixed culture can be partly attributed to the growth of the plants in monoculture and partly to species interactions. The relative yield deviated much more from the line of equal performance in the high nutrient situation than in the low nutrient treatment.

Only in *Festuca* in high nutrient conditions the turnover variable F_{dlv} (fraction of dead leaves) was affected when grown together with different species (Table 4). However, the level of significance was low, which indicates that competition had only some effect on this variable. In the N20 treatment, where both *Festuca* and *Anthoxanthum* were overtopped by *Holcus*, the SLA and SSH of *Festuca* and *Anthoxanthum* rose significantly as a result of competition (Figures 4 b,d, Figures 5 b,d, Table 4).

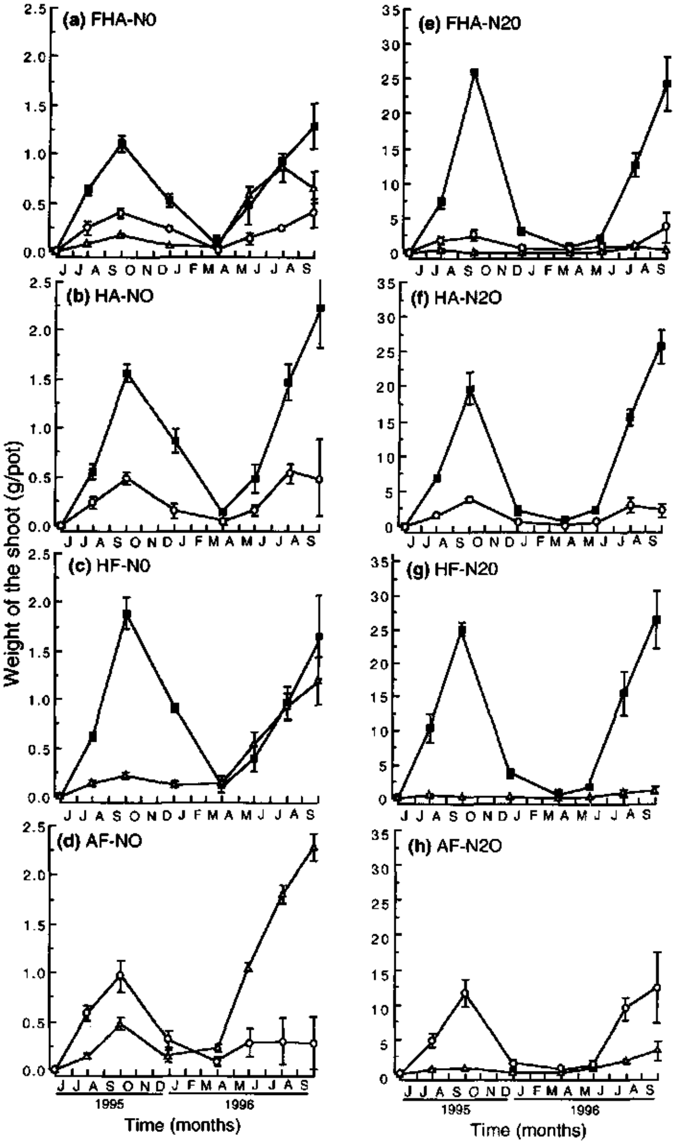

Figure 6. Shoot dry weight in 3-species mixture (FHA) and 2 species mixtures (HA, HF, AF) at low (N0) and high (N20) N supply. H, *Holcus lanatus* (■); A, *Anthoxanthum odoratum* (**O**); F, *Festuca ovina*(Δ). Error bars indicate ± 1 SE (n=4)

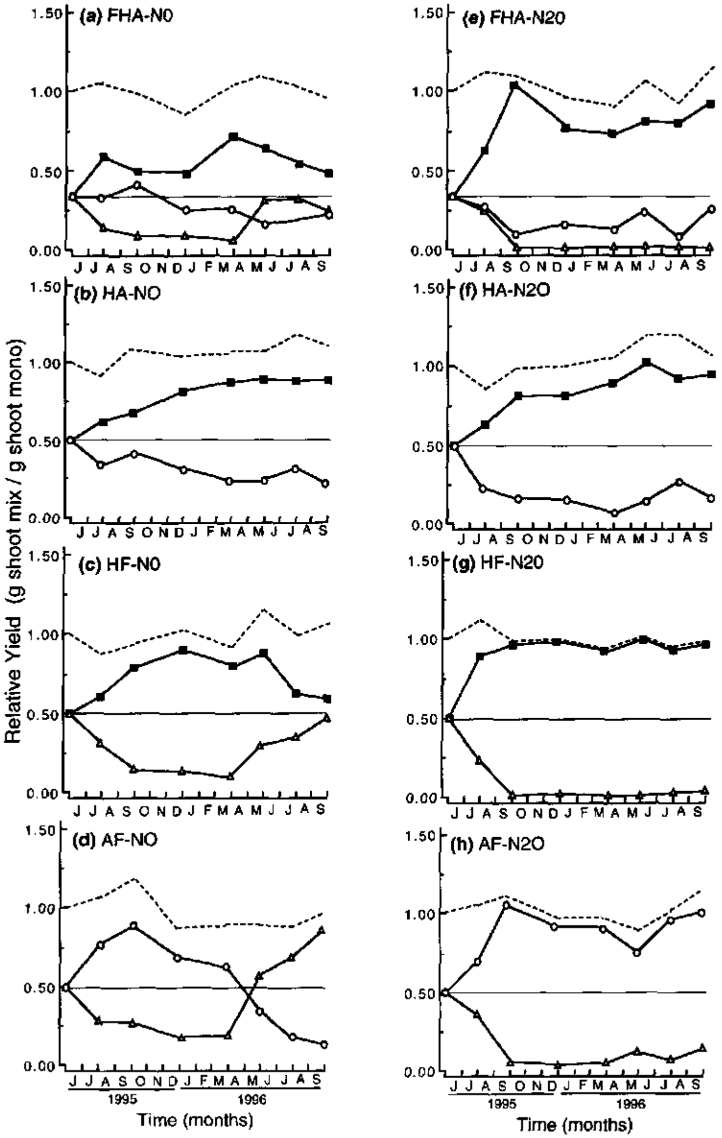

Figure 7. Relative yield in 3-species mixture (FHA) and 2 species mixtures (HA, HF, AF) at low (N0) and high (N20) N supply. H, *Holcus lanatus* (■); A, *Anthoxanthum odoratum* (O); F, *Festuca ovina*(Δ); Relative Yield Total (--------) . The thin horizontal line indicate the level where individuals in the mixed competition treatments have the same biomass as in the monoculture treatment.

Discussion

Experimental design

Conclusions based upon a single density replacement experiment cannot be uncritically extrapolated to estimate absolute competitive hierarchies among species, because competition depends on density and initial plant size (Connolly 1986, 1988). However, a replacement design does give correct information about competition between the species at that density and for that initial plant size (Shipley & Keddy 1994) and is therefore appropriate for studying competition in a comparative way (time, nutrients). The competition index we opted for (Relative Yield) was therefore used to compare the competitive state of the species in the experiment and not to rank the competitiveness of the species.

Our results demonstrate another effect that hampers the search for absolute competitive hierarchies within perennial species. Because of the change from short-term to long-term dominance in the competing perennial species, the results greatly depend on the duration of the competition experiment. In our view it would be better to abandon the search for absolute competitive indices in perennials and instead to search for species traits that determine competitive success in a certain environmental condition.

The effect of nutrients on the competitive asymmetry

According to the definition of Shipley & Keddy (1994), competition between species is asymmetrical when the relative yield (RY) of the dominating species exceeds 0.5, and concomitantly the subordinate species must have a RY below 0.5 (in two-species mixtures). Whether the competitive asymmetry is increasing or decreasing is indicated by the deviation from the 0.5 RY line. From Figure 7, it can be concluded that the competition between the 3 species is asymmetrical and that in all species combinations, competitive asymmetry is greater at the high nutrient supply. This also holds when the effect of mowing is excluded and only the first season is evaluated. Therefore it can be concluded that results of this experiment confirm the findings of Keddy et al. (1997) and support the theory of Grime (1979), who hypothesized that competition is more intense at high nutrient levels, which might explain the low species diversity in nutrient-rich grassland systems.

The reason for the increase in competitive asymmetry might be that competition for light, which is relatively more important in high nutrient conditions (Wilson & Tilman 1991), can be considered as more asymmetrical

(Grace 1995), probably because the directional nature of light makes it easier to monopolize than nutrients (Huston & DeAngelis 1994).

Competitive response of SLA, SSH and leaf turnover

Specific leaf area (SLA), specific shoot height (SSH) and leaf turnover can be considered as important traits determining successional position of species with respect to nutrients (Berendse & Elberse 1990, Elberse & Berendse 1993). Our results show that leaf turnover was generally not affected by the type of competitor. Only in the high nutrient treatment was leaf turnover of *Festuca* affected by the competitive treatment. However, this can be seen more as an effect of the competition than as a competitive response since *Festuca* was seriously over shadowed by its competitors.

Competitive response in SSH and SLA was found in *Festuca* and *Anthoxanthum* under nutrient-rich conditions, where both species were overtopped by *Holcus*. Rice & Bazzaz (1989) found longer plants and higher SLA at lower radiation levels in *Abutilon theophrasti*, which indicates that the reduction in light or a change in light quality might have caused change in both architectural parameters. In our experiment the competitive response of SSH and SLA of *Festuca* and *Anthoxanthum* was the same. The value of the SSH and SLA in *Anthoxanthum* increased even up to the level of *Holcus* at high nutrient availability. However, both height and leaf area remained much lower because of the smaller biomass of the shoot and leaves. This indicates that the plastic responses were insufficient to challenge *Holcus*, though they probably reduce the competitive asymmetry to some extent.

The species we studied were from different successional stages and were very different in their SSH and SLA, which limits the role of the competitive response. It is conceivable that competitive response is more important in reducing the competitive asymmetry of species that are more similar than those we studied.

Effect of seasonal change on SLA, SSH and leaf turnover

In both fast-growing species the SLA fluctuated with the season, being generally lowest in winter time. This contrasts with the findings of Rice & Bazzaz (1989) and Olff (1992), that SLA increased when light was reduced. One possible explanation for our finding of a higher SLA in summer is that the self shading effect is greater in summer if the leaf area index (LAI) is high. But the same pattern was also observed in the low nutrient treatment, where the

LAI remained low (LAI is approx. 1.0). These leaves certainly intercepted more light in summer than in winter. Horie et al. (1979) and Kropff & Van Laar (1993) found that the SLA is affected not only by light but also by temperature, since temperature governs leaf expansion whereas radiation governs photosynthesis. When leaf expansion is limited and the photosynthesis continues, the carbohydrates in the leaves increase resulting in a lower SLA (Alberda 1957). Since the effect of light would have given opposite results (high SLA in winter and low SLA in summer), we conclude that temperature is the main driving force for SLA changes over the year.

The seasonallity of the SSH (specific shoot height) is partly ascribable to the mowing treatment at the beginning of October (1995) and partly to mortality in winter resulted in a lower SSH in spring. There is a striking difference between the species with respect to mortality in winter. *Holcus* and *Anthoxanthum* lost nearly all the leaves that resprouted after mowing, whereas *Festuca* leaves stayed green and the amount of leaves even increased during winter.

In general, it can be concluded that interspecific differences in both architectural characteristics (SLA and SSH) lessen during winter, whereas the leaf survival in winter of *Festuca* was high compared to both faster growing species, which might imply that species from a nutrient-poor habitat (represented in this experiment by *Festuca)* are superior in surviving and growth during winter.

Analysing interspecific competition

Productivity in the high nutrient treatment was 1000-1600 g m^{-2} $year^{-1}$. At this level of fertility we expected *Holcus* to be the superior competitor, with *Anthoxanthum* second and *Festuca* third. The results were as expected in all the species combinations. Species such as *Holcus* that are adapted to nutrient-rich environments have a strong advantage in this competitive situation for three reasons: firstly, the higher RGR gives *Holcus* an advantage at the time when the interaction between the species starts; secondly, it has a higher specific shoot height (SSH) which enables the plant to grow taller per gram of shoot biomass; and thirdly, its higher SLA facilitates the production of more leaf area per g leaf. All three properties are important characteristics enabling the plant to monopolize light.

In the low nutrient treatment the competitive ranking were less clear cut. At the end of the first season the sequence was the same as in the high nutrient treatment; i.e. species from a nutrient-rich environment were superior. It seems likely that the higher RGR of these fast-growing species enabled them to exploit the space above and below the ground more quickly. However, in contrast with the high nutrient treatment, the level of competitive asymmetry was reduced; the result was less difference between the species at the end of the first season.

In the second year, *Festuca* showed a remarkable recovery (as indicated by the RGR of the shoot) in the low N treatment in all species combinations, even out-performing *Anthoxanthum*. This unexpected comeback needs an explanation. According to current theory, species adapted to nutrient-poor environments are characterized by a low biomass turnover, which results in lower rate of nutrient loss (Grime 1979, Berendse & Elberse 1990, Aerts et al. 1990, Aerts 1995) and make them more efficient in their nutrient economy. However, the biomass of *Festuca* increased markedly in early spring. The timing of this event suggests that other processes might be involved.

Rorison et al. (1981) pointed out that the ability of *Festuca* to take up ammonium at low temperatures might explain its superior growth in winter. Although it is difficult to interpret the soil data (Figure 1 a,b), because ammonium can be converted to nitrate during the incubation, the results suggest that nitrate was the main nitrogen source (indicated by the large difference between the incubated and the direct measurements). This makes it unlikely that the process described by Rorison et al. (1981) determines the recovery of *Festuca*.

Another explanation of this phenomenon might be found in differences in carbohydrate storage capacity among the species. However, there is no evidence for a larger storage capacity in *Festuca* compared to faster-growing species such as *Holcus* or *Lolium* (Atkinson & Farrar 1983, Steen & Larsson 1986, Kraus et al. 1994). Moreover, at the beginning of winter, in the mixed treatments, the total biomass of the faster growing species was much higher, suggesting that their absolute storage capacity is higher which would lead to better regrowth in spring for these species.

Besides a more efficient nutrient economy, another benefit of a low biomass turnover is the survival of leaves during the winter, as observed in *Festuca*. Having leaves in wintertime allows photosynthesis during winter and early spring (Woledge et al. 1989) and the availability of old leaves in spring put *Festuca* in a better starting position for regrowth. Since the performance of species in competition can be determined largely by initial biomass (Connoly 1986, Kropff & Van Laar 1993) we believe that the success of *Festuca* in the low nutrient treatment of this experiment, can be attributed principally to winter survival and winter- and spring photosynthesis.

Conclusions

Our results support Grime's (1979) theory that competitive asymmetry is greater in fertile conditions. We suspect that the causal factor is the directionality of the light, which is easier for a superior competitor to monopolize than nutrients. The competitive response of the important traits SLA, SSH, and leaf turnover was limited and not enough to alter the competitive relations in the experiment. However all three traits showed important seasonal changes, resulting in better survival and growth abilities during winter in favour of species adapted to a nutrient-poor environment. This fact, is often neglected in the literature, may contribute to a better understanding of succession.

4

Competition for light and nitrogen among grassland species: a simulation analysis

Adapted from P. Schippers & M.J. Kropff (accepted in Functional Ecology)

Abstract

A plant competition model to analyse the competition among perennial grassland species was developed and used to find out whether complex perennial competition processes could be simulated accurately on the basis of ecophysiological principles, what crucial parameters and processes determine succession and how spatial heterogeneity affects inter-species competition for light and nitrogen.

In order to test model performance, simulation results were compared with results of a two-year replacement experiment involving *Holcus lanatus*, *Anthoxanthum odoratum* and *Festuca ovina*. Sensitivity analyses were performed to evaluate the importance of processes and parameters. Furthermore, to evaluate the effect of patchiness on vegetation development, simulations with a spatially explicit version of the model were studied.

The model's great sensitivity to plant height, specific leaf area and turnover and the large interspecific differences indicate that these are the key parameters determining competition between the species studied. *Festuca's* low shoot turnover enabled it to survive the winter better and gave it a head start in spring; this resulted in an unexpected come-back after winter in the second year.

The model's ability to simulate complex perennial competition processes as observed in the experiment indicates its potential for analysing vegetation processes related to succession. Simulations with a spatial explicit version of the model showed that patchiness of the species reduced competitive asymmetry, especially under nutrient-poor conditions. This indicates that when patchy communities are studied, space should be incorporated in the model.

Key words: Competitive asymmetry, longevity, fertilization, mowing, patchiness, senescence, shoot-to-root ratio, simulation model, space, spatial model, specific leaf area, succession, reserves, turnover

Introduction

The availability of soil nutrients is a key factor determining species composition in temperate grasslands (Grime 1979, Tilman 1985, Berendse & Elberse 1990). Plant species, adapted to different levels of nutrient availability have different properties. Two of the most important plant traits of species adapted to nutrient-rich grasslands are a large specific leaf area (SLA in dm^2 leaf/g leaf) (Poorter & Remkes 1990, Hunt & Cornelissen 1997) and a relatively tall architecture (Elberse & Berendse 1993). In contrast, species adapted to nutrient-poor environments are characterized by a slower biomass turnover (Grime 1979, Tilman 1985, Berendse & Elberse 1990, Schläpfer & Ryser 1996) which is responsible for a more efficient nutrient economy in the long run, since this process is the result of the balance between nutrient capture and loss (Berendse & Elberse 1990). It follows that potential plant height, SLA and biomass turnover are key traits determining the successional position and thus determine the competition between species from different successional stages.

In Chapter 3, a medium long-term competition experiment was conducted on the grasses *Holcus lanatus* L., *Anthoxanthum odoratum* L. and *Festuca ovina* L. at high and low nutrient levels. They reported a remarkably fast succession in favour of *Festuca* after the winter in nutrient-poor conditions. In this time period the SLA and plant height of the two fast growing grasses (*Holcus* and *Anthoxanthum*) declined but their turnover increased sharply. In contrast, in *Festuca* these parameters showed only a small response to the seasonal change. These results raised the question of whether the seasonal changes in the key parameters mentioned are enough to explain *Festuca's* strong competitive ability in nutrient-poor environments.

In the last decade, ecophysiological simulation models have improved understanding of multi-species competition. For instance, Ryel et al. (1990), Beyschlag (1990) and Barnes et al. (1990) used a multi-species canopy model to analyse several aspects of light competition and Kropff & Van Laar (1993) developed the 'INTERCOM' model which was able to simulate competition for light and water in crop-weed associations. More recently, Thornley et al. (1995) and Schwinning & Parsons (1996) have developed models that describe the long term competition between the perennial species clover (*Trifolium repens*) and rye grass (*Lolium perenne*).

Many studies of plant population dynamics have used spatially explicit models when analysing plant competition (Moloney & Levin 1996, Crawley & May 1987). Most ecophysiological plant competition models, however, assume that interacting species are well mixed. Though realistic for mixed canopy experiments and simple agricultural systems, this is not true for complex vegetation. Here, space is an important factor because plant competition occurs locally and vegetation is often patchy. This implies that some species may not compete with some others in the same community (Silvertown et al. 1992). To analyse this effect of patchiness a spatially explicit ecophysiological model for competition is needed.

This chapter describes a spatially explicit ecophysiological model (VEGPOP1) we developed to analyse competition between perennial species. We used the model to answer the following questions: (1) Can complex perennial competition processes as found in the competition experiment described in Chapter 3 be simulated accurately on the basis of ecophysiological principles? (2) Are plant height, SLA and biomass turnover indeed key parameters determining competition in different successional stages? (3) How does spatial heterogeneity in species distribution affect the competition?

Competition experiment

The competition experiment (Chapter 3) whose data we used had been conducted in an unheated half-open glasshouse (roofed but walls were 50% open). The grasses *Holcus lanatus*, *Anthoxanthum odoratum* and *Festuca ovina* were grown at two nutrient levels (for detailed description see Chapter 3). Daily minimum and maximum temperatures were recorded in the greenhouse (in Wageningen The Netherlands). The daily radiation receipt in the greenhouse was calculated from measurements from a nearby meteorological station (Wageningen) and the greenhouse transmission (Figure 1).

The experiment, which lasted two growing seasons and a winter, was carried out according to the De Wit (1960) replacement design, with one mixed treatment (50%-50%) for all species combinations, including a three-species mixture. This was done by planting six seedlings per square 3-liter pot containing nutrient-poor sandy soil (16 × 16 cm^2 surface area). Two nutrient levels were established: N0 and N20. In the N20 treatment, 3.14 g NPK fertilizer (15% nitrogen, 12% phosphorus and 24% potassium) was applied each year in July, equivalent to an input of 20 g of nitrogen m^{-2}. No fertilizer was applied to the N0 treatment. The nitrogen mineralization of the soil was measured during the experiment (Figure 1).

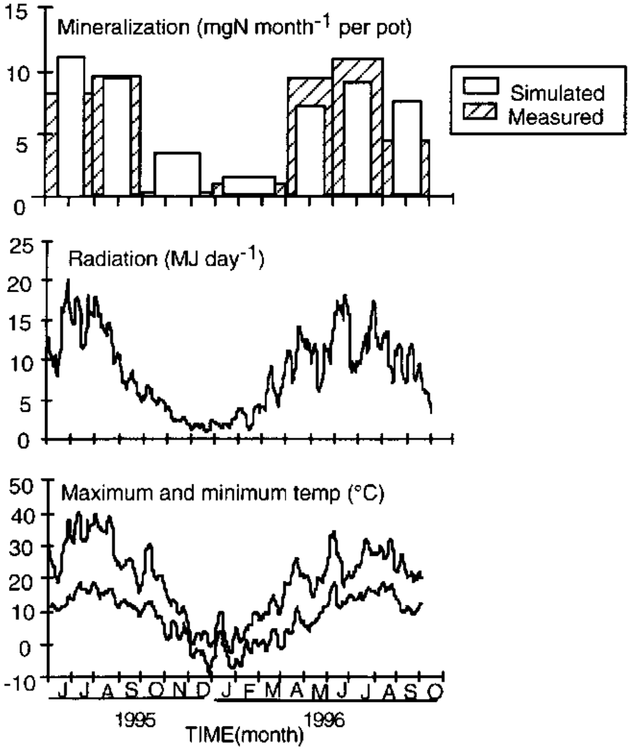

Figure 1. Mineralization, radiation and temperature in the greenhouse during the experimental period. Every point in both lower graphs represents a weekly mean.

Seven pots from the same competition treatment (1 for each sampling date) were placed together to form a 'plot' of 17.9 dm^2 containing 42 plants. To minimize serious edge effects, green netting with a light transmission of 10% was put around each pot so that it was kept 10 cm below the top of the canopy. The pots were watered frequently during the experiment, to prevent water stress. Since the experiment represented a grassland community, all plants were clipped to a height of 3 cm in October at the second harvest. Seven harvests were taken at two-month intervals (3 months in winter). At each harvest we measured the dry weights of plant parts and also the leaf area and plant height. Root weight was only measured in the monoculture treatments. Nitrogen mineralization of the soil was measured during the experiment using the *in situ* method described by Raison et al. (1987).

Model description

The model we develop is called 'VEGPOP1'. It is a simulation model, written in standard Fortran 77, which simulates a community of several species. The main state variables in the model are dry weights of flowers, shoots, roots and reserves of the defined species. In the model species compete daily for light and nitrogen. The model simulates the dry matter production and the nitrogen cycle of the system for the plant and soil compartments (Figure 2).

Light absorption and growth

In the model 'VEGPOP1' species growth is determined by the amount of photosynthetically active radiation (PAR) each species absorbed (Schapendonk 1998). The absorption of PAR by individual species follows the complex routine of Kropff & Van Laar (1993), but with the process strongly relying on equations 1 and 2 given below.

$$A_t = I_t \cdot (1 - e^{-\sum_1^n k_i \cdot L_i}) \qquad \text{equation (1)}$$

Where: A_t = total absorbed radiation (PAR) by all the species in a certain horizontal layer (MJ m^{-2} d^{-1}), I_t = the amount of (PAR) at the top of a horizontal layer (MJ m^{-2} d^{-1}), k_i = extinction coefficient of species i (-), L_i = leaf area index of species i in the layer (m^2 leaf m^{-2} area)

For each species i, the absorbed radiation (A_i in MJ m^{-2} d^{-1}) is calculated according to:

$$A_i = A_t \left[\frac{k_i \cdot L_i}{\sum_1^n k_i \cdot L_i} \right] \qquad \text{equation (2)}$$

In the model the daily net dry matter growth per species can be calculated as follows, assuming that the maintenance respiration is proportional to plant biomass (Penning de Vries 1975):

$$\frac{dW}{dt} = F_n \cdot F_g \cdot F_c \left(E \cdot A - W \cdot M \cdot F_m \right) \qquad \text{equation (3)}$$

Where: A = Absorbed Radiation (PAR MJ d^{-1} m^{-2} $species^{-1}$), E = light

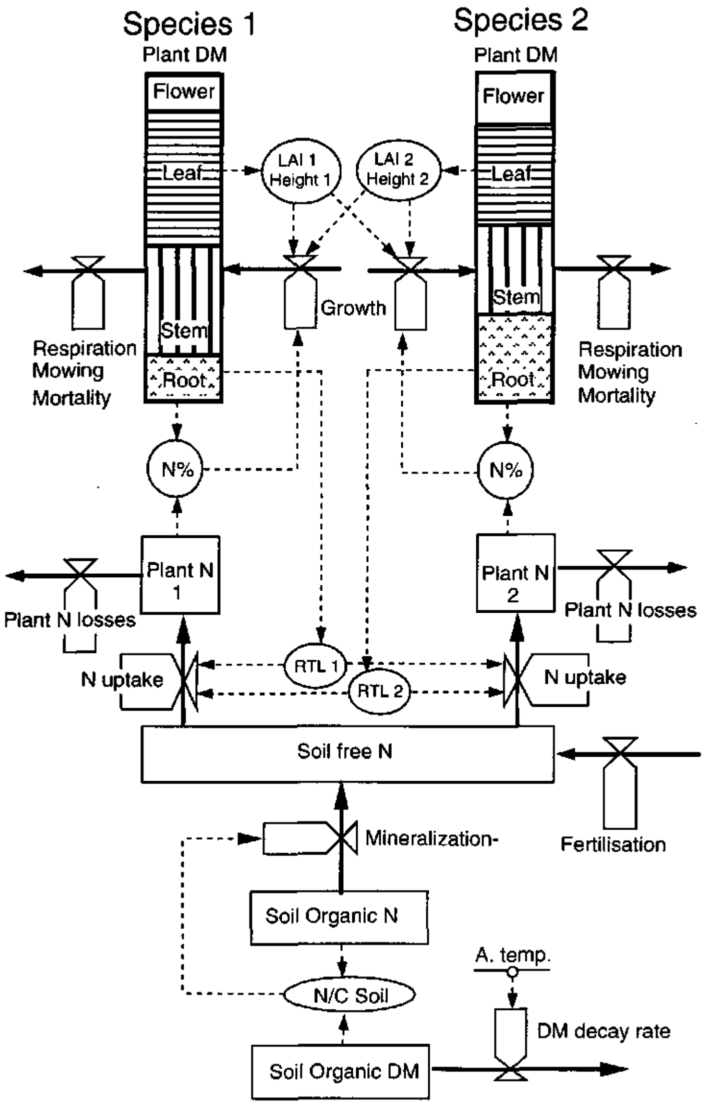

Figure 2. Flow diagram summarizing the competition for light and nitrogen of two plant species in the VEGPOP1 model. (N = nitrogen, C = carbon , DM = dry matter, LAI = leaf area index, RTL = root length).

conversion coefficient (= 4.77 g CH_2O MJ^{-1}), W = dry weight of the plant (g m^{-2}), M is maintenance respiration rate (= 0.015 g CH_2O g DM^{-1} day^{-1}), F_m = temperature-dependent factor of the maintenance process, F_c = Conversion factor (= 0.7 g DM g CH_2O^{-1}), F_n = factor that determines the growth reduction caused by nitrogen stress and F_g = temperature-dependent factor for plant growth.

The same general plant parameters were used for all species as they do not differ greatly among grasses (Table 1). The temperature dependence of both photosynthesis and maintenance respiration were modelled according to the relation published by Larcher (1976, see also appendix A). The growth reduction caused by nitrogen stress (F_n) was modelled according to Seligman & Van Keulen (1981) and is dependent on the actual nitrogen concentration of the shoot N_a (g N g^{-1} DM). If this exceeds a critical value, N_c, growth is not reduced. Below this value, growth rate decreases linearly with N concentration:

$$F_n = \frac{N_a - N_m}{N_c - N_m} \qquad \text{and } 0<F_n<1 \qquad \text{equation (4)}$$

Where: N_m = the minimum N concentration (g N g^{-1} DM).

Generally, N_c depends upon the maximum N concentration (N_x) (Spitters 1989) of the shoot. In turn, the latter parameter is related to the age of the shoot (Wilman et al. 1994). The process of aging depends on temperature and is well described by the temperature sum (Goudriaan & Van Laar, 1994). Since the model keeps track of shoot age classes of each species on a daily basis (see turnover section), the average maximum nitrogen concentration is estimated assuming that the N_x of age classes declines linearly with the temperature sum from young to old leaves. From this maximum nitrogen concentration, the critical N concentration (N_c) is derived by multiplying $N_x(t)$ by 0.65 (Spitters 1989). We assigned a minimum nitrogen (N_m) concentration of 0.5% (Spitters 1989).

Allocation

In the model the net dry matter growth of the whole plant (dW/dt) is allocated among different plant organs. Four different plant pools are distinguished: flowers, shoots, roots and reserves.

Table 1. Parameters used in the VEGPOP1 model of the species *Holcus lanatus*, *Anthoxanthum odoratum* and *Festuca ovina*.

Symbols	Description(unit)	*Holcus*	*Anthox.*	*Festuca*	Source*)
Physiological parameters					
E	Light conversion coef. (g CH_2O/MJ PAR)	4.77	4.77	4.77	(P1)
k	Extinction coefficient	0.6	0.6	0.6	(L2)
M	Maintenance respiration (g CH_2O/g DM d)	0.015	0.015	0.015	(P3)
F_c	Conversion factor (g DM/gCH_2O)	0.7	0.7	0.7	(P4)
Allocational parameters					
F_l	Fraction leaves (g leaves/g shoot)	0.48	0.52	0.68	(M5)
F_m	Minimum shoot fraction	0.32	0.38	0.44	(M5)
F_x	Maximum shoot fraction	0.72	0.82	0.87	(M5)
Parameters determining reserve allocation					
R_s	Reserve fraction of the shoot (g res./g sh.)	0.2	0.2	0.2	(M6)
R_r	Reserve fraction of the root (g res./g root)	0.05	0.05	0.05	(M6)
R_m	Minimum reserve fraction of R_s and R_r	0.5	0.5	0.5	(L7)
T_s	Temp. sum (mobil. reserves starts) (°C day)	289	289	289	(L7)
T_e	Temp. sum (mobil. of reserves ends) (°C day)	422	422	422	(L7)
Parameters determining turnover					
T_{sh}	Temp. sum determ. shoot longevity(°C d)	1265	650	1965	(M8)
T_f	Temperature sum of freezing (°C d)	97	163	655	(M8)
F_r	Root mortality factor (d^{-1})	0.00371	0.00341	0.00282	(O8)
Parameters determining nitrogen economy					
N_y	Maximum N conc. of a young shoot (gN/gDM)	0.04	0.04	0.04	(L 9)
N_o	Maximum N conc. of an old shoot (gN/gDM)	0.01	0.01	0.01	(L9)
N_c	Critical N fraction of current shoot (N_x)	0.65	0.65	0.65	(P10)
N_r	N concentration of the Roots (gN/gRT)	0.006	0.006	0.006	(P10)
N_m	Minimum N conc. of the plant (gN/gDM)	0.005	0.005	0.005	(P10)
Architectural parameters					
SRL	Specific root length (m/g root)	316	306	380	(M11)
SLA	Specific leaf area dm^2/g leaf)	see Fig. 3			(M8)
H	Height (cm)	see Fig. 3			(M8)
R	Height:Width Ratio	3.4	2.2	2.1	(M11)
V	Volume per gram shoot (l/gDM shoot)	1.13	0.53	0.61	(M11)

*) Source:

P = general plant value, L = *Lolium perenne* value used, M = measured on the same species, O = obtained by optimizing, (number = first authour (year): 1 = Lövenstein (1992), 2 = Schapendonk (1998), 3 = Penning de Vries (1975), 4 = Penning de Vries (1974), 5 = Chapters 2 & 3, 6 = Atkinson (1983), Steen (1986), 7 = Alberda (1955), 8 = Chapter 3 monoculture data, 9 = Wilman (1994), 10 = Spitters (1989), 11 =Chapter 2.

The allocation to the reproductive organs is assumed to be a constant fraction of the assimilates produced during flowering time and seed filling. The flowering period is determined by the temperature sum since January 1 and was obtained from field observations (Table 1). This simple system generates partitioning patterns for reproductive organs that correspond fairly well with those described in Chapters 2 and 3. We set the allocation parameter at 0.07, which is a common parameter for perennial plants (Harper 1977).

Plants store part of their assimilates as reserves which can support regrowth after cutting and in early spring (Alberda 1955). The reserves in grass shoots are about 20% of the shoot dry matter and about 5% in the roots, except during regrowth (Atkinson & Farrar 1983, Steen & Larsson 1986). Reserves are often not used completely but often plants use only half of the reserves for regrowth (Alberda 1955).

The above described system was implemented in the model in the following way. The increase or mobilization of the reserves pool is dependent on the actual fraction of reserves (F_r). Once this concentration exceeds a critical value F_i (F_i =0.2 for the shoot and 0.05 for the root), the reserves are mobilized. When F_r is less than F_i, assimilates are stored as reserves. This will result in reserve fractions (F_r) near the critical fraction (F_i). By varying this critical fraction over time, reserve dynamics (cf. Alberda 1955) can be simulated. We did so by decreasing the critical fraction to half the normal value during a 14-day period after mowing and during the regrowth period in spring. The regrowth in spring is determined by the temperature sum (above 0°C) (Table 1). This procedure achieves a mobilization of reserves during these defined periods and an increase in reserves thereafter. Since the grasses used in this study do not develop storage organs, the reserves are integrated in the shoot and root compartment. To achieve this, the weight of the reserves is added to the organ weight before the size-related parameters (LAI, height, root length) are calculated.

Given that the shoot:root ratio of a plant is strongly related to the plant's nitrogen concentration (Brouwer 1962) and knowing that a linear relation between the shoot fraction and the nitrogen concentration (over a defined range) had been reported by Levin et al. (1989), we made allocation to root and shoot in the model linearly dependent upon the nitrogen concentration of the shoot. If the shoot fraction exceeds the shoot fraction calculated on the basis of the nitrogen concentration, more of the assimilate is allocated to the roots and vice versa. The shoot fraction is allowed to vary between a maximum (F_x) and a minimum (F_m). Both values were estimated by taking the largest and smallest measured shoot fraction from the data of Chapter 3. The critical shoot fraction, F_e, can be estimated as:

$$F_e = F_m + (F_x - F_m)\frac{(N_a - N_m)}{(N_x - N_m)} \qquad \text{equation (5)}$$

Where: F_m = the minimum shoot fraction, F_x = the maximum shoot fraction, N_a = the actual N concentration of the shoot (gN gDM^{-1}), N_m = minimum N concentration of the shoot, and N_x = the maximum N concentration of the shoot.

Architecture

The leaf fraction of the shoot (F_l in g leaves / g shoot) and the specific root length were based on measurements obtained in Chapter 2 on the same grass species as used in the present study. The root length was determined by multiplying the root weight including root reserves by the specific root length. The model calculates leaf area by multiplying the leaf weight including leaf reserves by the specific leaf area (SLA). During the simulations we used measured values of SLA and plant height of the monocultures (Figure 3).

Nitrogen uptake

The nitrogen uptake in the model follows the description of Van Keulen & Seligman (1987). In this approach the daily amount of nitrogen taken up depends on the species demand, the amount of available nitrogen in the soil and the root length of the species. The demand is defined as the difference between the plant N concentration and the maximum plant N concentration. The amount of available nitrogen that a species can capture depends on the amount of free nitrogen in the soil and the proportion of root length of a species (for a precise description, see appendix B).

Survival of shoot and root

The turnover of plant parts is important in long-term competition (Berendse & Elberse 1990). Ageing is often related to the temperature sum (Goudriaan & Van Laar 1994). The turnover of the shoot was therefore defined in the model by the number of degree-days that tissue can remain alive (T_{sh}). Separate cohorts of the shoot were modelled daily. This means that the model keeps

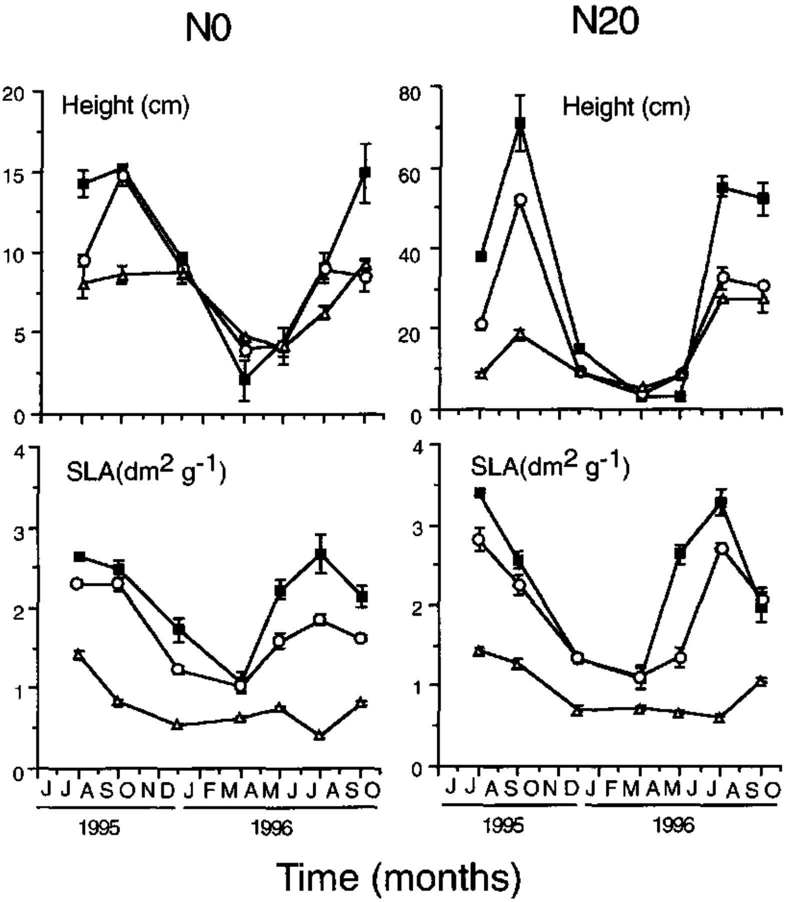

Figure 3. Height and specific leaf area (SLA) during the experimental period for three grassland species measures in the experiment done in Chapter 3. N0= low nutrient conditions no nutrient applications, N20 high nutrient conditions application of 20g N m^{-2}. ■ = *Holcus lanatus*, **O** = *Anthoxanthum odoratum*, Δ = *Festuca ovina*.

track of age classes of shoots, and the temperature sum these age classes encounter during their life. When the temperature sum of a given a age class was greater than T_{sh} this cohort dies. This method was unable to simulate the high mortality caused by frost during winter, however, so an extra routine had to be developed. In winter, a constant temperature below 0°C affects the leaf longevity L (days) as follows:

$$L = \frac{-T_f}{T_a} \qquad \text{and } Ta<0 \qquad \text{equation (6)}$$

Where: T_a = average daily temperature below 0 °C, T_f = species-specific parameter describing the period (expressed as temperature sum below zero in °Cd) that plant tissue can survive temperatures below 0 °C.

The leaf and dead leaf fractions from the monoculture treatments of the experiment were used to estimate the parameters of the system. Since roots can live much longer than shoots (Troughton 1981, De Willigen & Van Noordwijk 1987), in the model their turnover dynamics are described by a turnover fraction per day. The turnover fractions were derived from root longevity values calibrated using the whole model. During the calibration, shoot and root biomass values were optimized by varying the root longevity. During the calibration procedure the model keeps track of individual root age classes per day.

Mineralization, fertilization and mowing

In the simulations presented here a simple first order decay of organic matter is used to describe N mineralization: the increase of soil free N equals:

$$\frac{dN}{dt} = C \cdot N_C \cdot T_a \cdot K \qquad \text{if } T_a>0 \qquad \text{equation (7)}$$

$$\frac{dN}{dt} = 0 \qquad \text{if } T_a<0$$

Where: C = C content of the soil (g C m^{-2}), N_C = N:C ratio of the soil (g g^{-1}), T_a = average temperature, K = decomposition rate (°C^{-1} d^{-1}). The parameter K is estimated from the total measured soil mineralization of the experiment and the average temperature above 0 °C (K = $1.56 \cdot 10^{-5}$) whereas the C concentration and the N:C ratio were measured in experimental soil (C = 792 g m^{-2}, N:C=20). The measured and simulated mineralization data are shown in Figure 1. Nitrogen can be added on a specified day; it contributes to the free N pool in the soil (Figure 2).

The mowing regime in model achieved a simulated biomass after mowing that matches the biomass obtained experimentally. As in the experiment in the model the cuttings were removed from the system.

Extended spatially explicit version

In common with many other model approaches, in this model too, space is represented by a lattice (Van Dorp et al. 1997, Moloney & Levin 1996). Each cell in this lattice can contain several competing species, which are presumed to be well mixed. Each species in the cell is characterized by the weight of the plant parts and the number of plants. Cell and field sizes can be adjusted, depending on the purpose of the model. The edge of the lattice can be made toroidal (the amount of biomass which grows over the edge of the lattice returns at the opposite side of the lattice) or reflecting (the amount of biomass which grows over the edge of the lattice returns to the cell of origin).

In the model, species height and ground cover are calculated from a simple spatial concept derived from the self-thinning law (Yoda et al. 1963). This law only holds when species have a constant specific volume (volume per shoot biomass) and a form which can be described by the height/width ratio. Only when both factors are constant during growth does the self thinning law lead to the −1.5 thinning curve. In the model, the specific volume of leaves and stems is an input parameter for each species. The height/area ratio is transformed to a height:width ratio, assuming that the area occupied by each individual is a square. From this framework and the number of plants, the height and covered area of every species in every cell can be calculated.

The height is calculated from the shoot weight per plant, which can be calculated from the shoot dry weight and the number of plants of this species per cell. If plants of a species are assumed to have the same form and species have a constant specific volume during their growth, the following relation can be derived for the height:

$$H = \left(R^2 \cdot V \cdot B\right)^{1/3} \qquad \text{equation (8)}$$

where:

H = height (dm), R = Ratio of height to width, V = Specific volume (dm^3 g^{-1}), B = biomass of the shoot (leaves + stems) of one plant (g DM).

Although this height description seems to uncouple height from stem investment this is not the case, because in the species parameterization the stem investment ($1.0 - F_l$, Table 1) is strongly related to the height to width ratio (R, Table 1).

Similarly, the area covered A (dm^2) by an individual plant can be calculated:

$$A = \left(\frac{V \cdot B}{R}\right)^{2/3} \qquad \text{equation (9)}$$

If the area covered by all plants of the same species exceeds the cell area, the surplus of shoot biomass is exported to the 8 surrounding cells, as are proportional amounts of roots, reserves and plant numbers (note: plant numbers are reals). The resulting in new clones in neighbouring cells have the same height as the mother plant (Figure 4). The parameters of R and V were derived from the experiment described in Chapter 2.

Quality check

The model we developed has many state variables and complex interactions, furthermore the model includes space and shoot age classes. To safeguard the quality of such a complex model we put much effort in creating range and balance checks throughout the program. The model checks the balance of nitrogen and of carbon by comparing the amount of total input (including the initial amount) minus the total loss with the actual amount that is represented in the state variables. This check includes all species and all the soil compartments in all cells. The maximum proportional difference permitted in the balance checks during the simulations was 0.001.

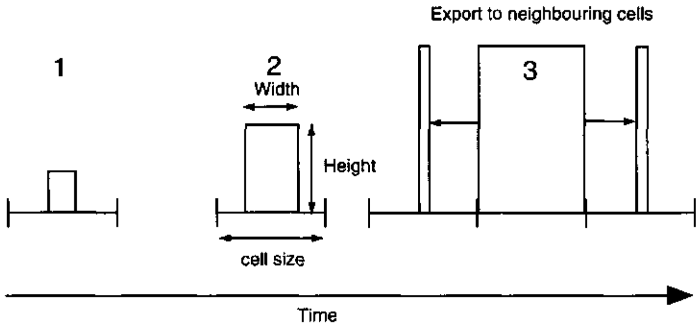

Figure 4. Height, area and export of a plant during growth in relation to the cell size of the spatially explicit version of the model.

Simulations

Simulating the experiment

Using the parameter values for the different species given in Table 1 and Figure 3, simulations were performed on a pot basis for all species in monoculture, and for two and three species in competition at two nitrogen levels The simulations were done using the standard version of the model (not spatially explicit) on an area similar to the area of experimental pots (16×16 cm^2) assuming maximum mixing. The simulations were initialized with six seedlings using the biomass of the seedlings planted in the experiment (*Holcus* = 0.56 mg, *Anthoxanthum* = 0.51 mg and *Festuca* = 0.35 mg). The mineralization was simulated on an area basis using the estimated decomposition rate (see section on mineralization). In the simulations we also used measured weather data (Figure 1) as well as measured mowing values.

Parameter sensitivity

Parameter sensitivity was studied in the mixture of *Festuca* and *Anthoxanthum* under the experimental conditions described. We chose this species combination because of the contrasting experimental results induced by the nutrient application. The sensitivity analysis was performed by increasing the value of one species parameter by 1%, to give a modified species (indicated with an *). Model sensitivity was defined as the relative change in performance of the modified species when a certain parameter was increased by 1%. Four combinations of species were analysed: modified *Anthoxanthum*-Festuca, Festuca*-Anthoxanthum, Anthoxanthum*-Anthoxanthum, Festuca*-Festuca* in the two defined nitrogen conditions. This yielded eight simulation series.

The effect of introducing patchy species distribution

To analyse the effect of spatial distribution on the species competition, the simulations were performed for a squared lattice of 12 × 12 cells with a cell size equal to the pot size used in the experiment. Every cell contained six plants. In total, 288 plants of each of the three species were distributed over the area. We varied the pattern of species distribution, so that we could analyse the effect of patchiness on the inter-specific competition. Patchiness was defined by the number of mixed cells that contained two plants of each of the three species. Other cells were parameterized with six plants of the same species. This resulted in a simple one-parameter system defined by the percentage of mixed cells. For instance, if the percentage mixing is 50%, the number of mixed cells (three species present) is 72 out of 144, with a further 24 cells containing six *Holcus* plants, 24 cells containing six *Anthoxanthum* plants and 24 cells containing six *Festuca* plants. This total of 144 cells was randomly distributed over the area.

Simulations were performed at high and low nitrogen levels and five percentages of mixing (0, 25, 50, 75, 100 %). The simulations were evaluated on day 275 in the second year. The average relative yields (simulated production of species in mix-culture / simulated production of species in monoculture) of three reruns with different random initialization were evaluated.

Simulation results

Simulating the monoculture experiment

The nutrient application resulted in a tenfold increase of the dry matter production in all the species. Shoot growth in the first season was overestimated for *Festuca* at both nutrient levels and for *Anthoxanthum* in the N0 treatment. The shoot production of *Holcus* was underestimated at both nutrient levels (Figure 5). At the high nutrient level the simulated regrowth after winter was underestimated in *Festuca* and the total final biomass was underestimated in *Holcus*. Root growth was not simulated very precisely, especially not in winter, where the measured root biomass remained constant whereas the simulated values decreased. In *Holcus* this led to an underestimation of the root biomass. These disparities probably arose because a simple turnover method was used in the simulations whereas the calibration was done by optimizing root longevity using root age classes. Furthermore, root longevity can only determine the decrease of the root biomass. This means that an underestimate of growth cannot be compensated for by changing the root longevity.

Simulating the mixed experiment

In the N0 treatment, the model results corresponded closely to the measured values (Figure 6). The model also simulated the change in dominance between *Anthoxanthum* and *Festuca* that occurred during winter. Under high nutrient conditions the maximum yield of *Holcus* was underestimated

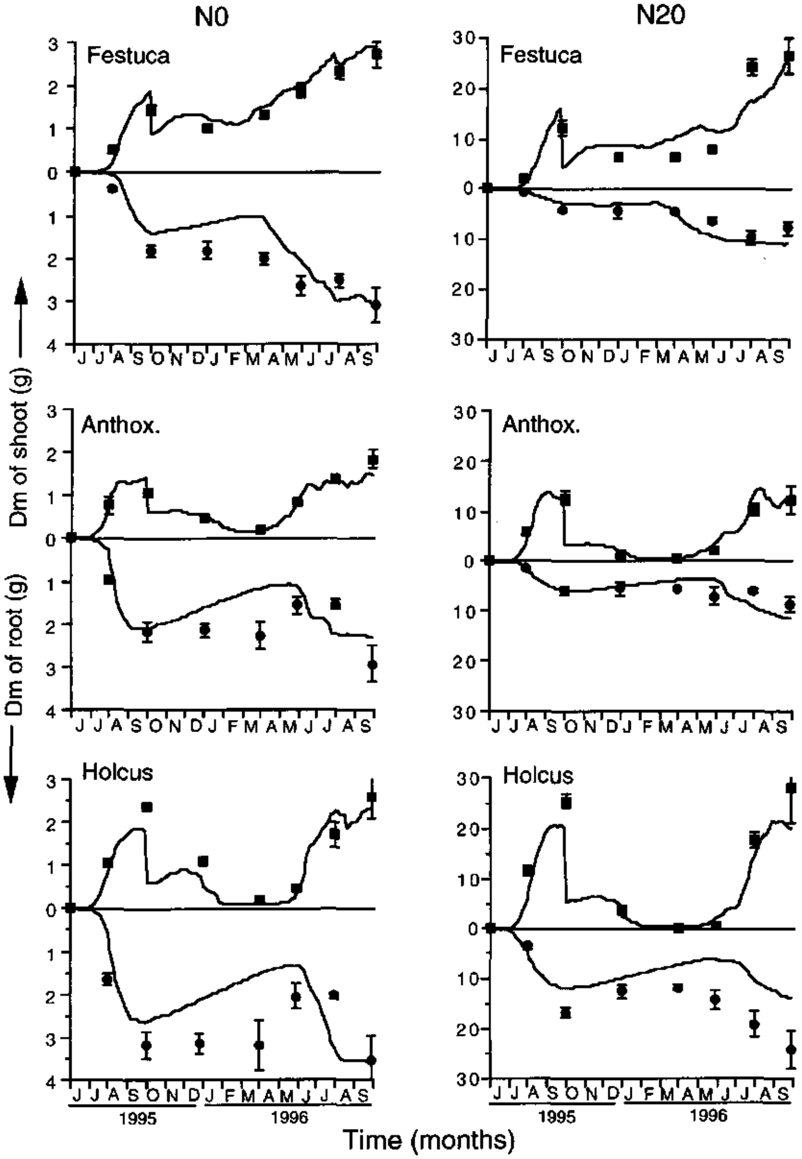

Figure 5. Simulated and measured values of the shoots and roots per pot of three grassland species in monoculture at two nitrogen levels: N0 natural background mineralization of 3.8 gN m^{-2} in the whole period, N20 as N0 but 20 gN m^{-2} added at the beginning of July. Error bars indicate ± 1 SE (n=4).

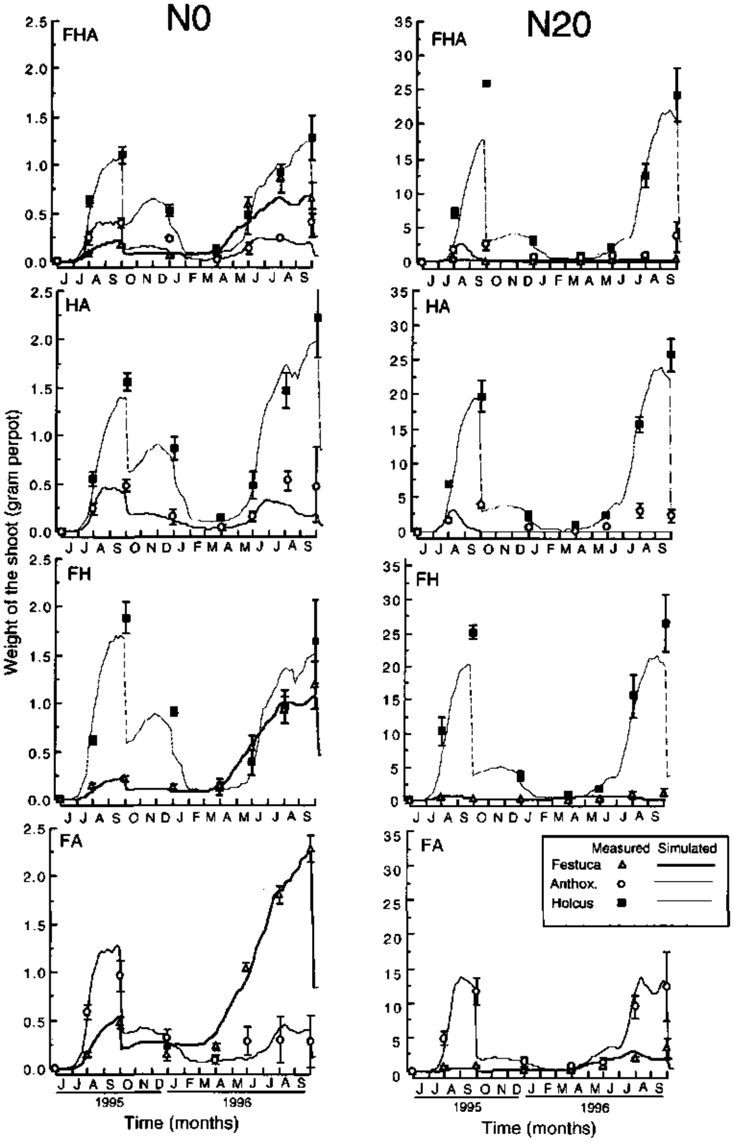

Figure 6. Simulated and measured dry matter values of the shoot of the mixed treatments of three grassland species at two nitrogen levels: N0 natural background mineralization of 3.8 g m^{-2} in the whole period, N20 as N0 but 20g N m^{-2} added at the beginning of July in both years. Error bars indicate ± 1 SE (n=4). F(Δ) = *Festuca ovina*, H(■) = *Holcus lanatus*, A(O) = *Anthoxanthum odoratum*.

by the model (Figure 6). *Anthoxanthum* died in the simulation run in the first season when *Holcus* was present whereas in the experiment it survived, reaching a maximum biomass of 2.6 g pot^{-1} at the end of the second season.

Parameter sensitivity

All the physiological parameters except for the maintenance respiration (M), belong to the three most sensitive parameters (Table 2). Of the parameters determining allocation, both F_l (the fraction of the shoot allocated to the leaves) and F_x, (the maximum fraction allocated to the shoot), were very sensitive in most competitive treatments. Parameters determining reserve allocation were generally insensitive. The temperature sum that determines shoot longevity, T_{sh}, was the most sensitive turnover parameter. It was crucial in the competition between *Anthoxanthum* and *Festuca* under low nutrient conditions and important in the competition between *Anthoxanthum* (A*-A) in the high nutrient conditions. All the parameters to do with nutrient economy were relatively insensitive.

The specific leaf area was the most sensitive parameter determining the species architecture. In the *Anthoxanthum* competition treatment (A*-A), at high nitrogen conditions, plant height was also crucial.

The effect of introducing patchy species distribution

Figure 7 depicts the results of the spatial simulations. The 0.33 line represents the situation where plant performance in the mixed treatment is the same as in the monoculture treatment. Above this line, plants performed better than in monoculture, whereas below this line they performed worse.

With the increase of the mixing percentage, *Holcus* became more dominant in the nitrogen-rich and nitrogen-poor conditions (Figure 7) at the cost of both other species. In the nitrogen-rich treatment *Anthoxanthum* almost disappeared at all levels of aggregation.

In the N0 treatment at 0% mixing the performance of the species did not deviate from the monoculture treatment, indicating that the inter-species competition was limited. This was not the case in the nitrogen-rich treatment. Here, *Holcus* performed much better than in the monoculture treatment, but both *Anthoxanthum* and *Festuca* performed worse.

Table 2. Parameter sensitivity during the intra and interspecific competition of *Anthoxanthum odoratum* (A) and *Festuca ovina* (F) expressed as the total biomass increase (%) of the species marked with '*' when the parameter of this species is increased by 1%. Values in bold are the 5 most sensitive parameters of that treatment. (Parameter description according to Table 1).

	Nitrogen level							
	N0 *)				N20 *)			
Par.	A*-A	A*-F	F*-F	F*-A	A*-A	A*-F	F*-F	F*-A
Physiology								
E	**7.1**	**13.2**	**4.1**	**1.5**	**22.2**	**3.7**	**10.0**	**19.7**
K_e	**4.6**	**11.0**	**3.3**	0.7	16.1	1.4	**7.1**	**14.8**
M	-1.0	-10.2	-1.2	**-0.8**	-5.2	-1.1	-1.8	-1.7
F_c	**5.5**	9.8	**3.4**	**1.1**	16.2	**2.7**	**8.2**	**15.9**
Allocation								
F_l	**7.3**	**12.1**	**4.1**	**1.6**	**21.3**	**2.5**	**9.3**	**19.5**
F_m	-0.3	5.9	-1.4	-0.5	-0.5	0.0	1.2	0.8
F_x	3.4	**14.5**	2.7	0.4	**25.4**	**2.4**	6.1	15.7
Reserve allocation								
R_s	0.9	1.8	0.2	-0.1	2.3	0.4	0.5	0.5
R_r	0.3	1.2	-0.2	-0.4	0.9	-0.1	0.0	0.0
R_m	0.0	-0.6	0.1	-0.5	0.3	0.0	-0.1	0.4
T_s	**0.1**	-0.5	-0.7	-0.5	-0.7	0.0	-0.1	**0.2**
T_e	**0.1**	1.3	0.1	0.0	0.0	0.0	0.0	0.0
Turnover								
T_{sh}	3.0	9.6	0.5	-0.3	**20.8**	1.9	1.4	3.2
C_f	-0.9	-3.3	0.0	**0.0**	-1.3	**-0.3**	0.0	0.0
F_r	-0.2	1.7	-0.3	-0.2	0.6	**0.1**	-0.1	0.0
Nitrogen economy								
N_y	-0.8	-0.1	0.0	-0.3	0.1	0.0	0.0	0.5
N_o	-0.1	-0.1	0.0	0.1	0.3	0.0	0.1	-0.3
N_c	0.7	-0.7	-1.1	-0.8	0.0	0.0	-0.1	0.0
N_m	-0.1	0.1	-0.5	-0.4	0.0	0.3	0.0	0.0
N_r	-0.3	0.2	-0.2	-0.4	0.0	0.3	0.0	0.0
Architecture								
H	0.2	0.5	-0.3	0.0	17.3	0.5	3.9	5.6
SRL	**1.6**	0.8	0.3	0.0	0.0	0.0	0.0	0.0
SLA	**7.3**	**12.1**	**4.1**	**1.6**	**21.3**	**2.5**	**9.3**	**19.5**

*) N0 = No additional nitrogen application, N20 = additional N comparable to 20 gN m^{-2}.

Discussion

Evaluating model performance

From the model description it is clear that a 'realistic' model has to deal with many processes, which makes the model complex. It was to overcome one drawback of complex simulation models, the increased likelihood of errors, that we equipped the model 'VEGPOP1' with balance checks for both nitrogen and carbon to minimize errors. Another drawback is that these models demand many species-specific parameters which are not always available or are too environmentally specific. For parameters that were not very species specific, we used general plant values or values observed in *Lolium perenne*. Other parameters were measured or calibrated using the monoculture data. This means that the monoculture simulations were not completely independent of the experimental data with which they were compared. The mixed treatments, however, were largely independent of the measurements. Our results show that, taking into account the complexity of the experiment (three species, two nutrient levels and two growing seasons) the model simulated the mixed species treatments well. The ranking of the species at the end of both seasons was simulated correctly and the simulated biomass values were of the right order of magnitude. This indicates the potential of the approach for analysing competition and succession in complex communities.

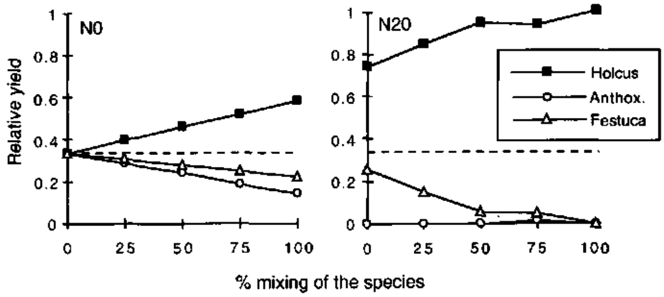

Figure 7. The simulated effect of patchiness on the relative yield of *Holcus lanatus*, *Anthoxanthum odoratum* and *Festuca ovina*. at high (N20) and low (N0) nutrient level. Relative Yield is the biomass of the species growing in a mixed system with 3 species present, compared with the performance of the species in monoculture. The dashed line indicates where performance of individual plant in the mixture equals performance of the plants in the monoculture. 100% mixing= no spatial heterogeneity, 0% mixing = all connected cells start as monoculture. Maximum SE at low nutrient level was 0 (n=3), maximum SE at nutrient rich conditions was 0.026 (n=3).

Mechanisms determining competition

The initial phase of competition in both nutrient conditions in our experiment and simulations is determined by the relative growth rate (RGR in d^{-1}). The RGR governs the initial expansion of the seedling, whereas the turnover is not important since tissue is still young. This is why in relatively short experiments species adapted to nutrient-poor habitats (with slow RGR) do worse, even in a nutrient-poor environment (Olff et al. 1990, Elberse & Berendse 1993).

Species such as *Holcus* that are adapted to nutrient-rich environments have a strong advantage in fertile conditions for three reasons: firstly, the faster RGR gives *Holcus* an advantage before interaction between the species starts; secondly, the taller shoot architecture (SSH) enables the plant to grow taller per gram of shoot biomass; and thirdly, its larger SLA facilitates the production of more leaf area per g leaf. All three properties are important characteristics enabling the plant to shade out competing neighbours.

Under low nitrogen conditions, winter and early spring appeared to be crucial periods favouring species such as *Festuca* from a nutrient-poor habitat. Elsewhere (Chapter 3) we hypothesized that the cause of the success of *Festuca* in the second year was the seasonal change in the values of SLA, plant height and turnover. The reduction in differences in the SLA and plant height among the species and the better winter survival of *Festuca* puts *Festuca* in a better starting position for regrowth in spring. The good match between experiment and simulations indicates that the differences in the key parameters as used in the model were enough to yield the same patterns as in the experiment, supporting our earlier hypothesis.

In addition to having a head start in spring, *Festuca* also starts regrowing earlier in conditions where its shoot weight equals that of its competitor (e.g. in competition with *Holcus*). This timing difference was not explicitly parameterized, which raises the question of how this difference in timing of the regrowth occurs. The explanation can be found in the low shoot:root ratios of *Anthoxanthum* and *Holcus* in early spring when a very small amount of leaves has to support the maintenance respiration of a large root system, leaving a small amount of assimilates for shoot regrowth. To our knowledge this mechanism has not been reported before and might be important determining the competition in mown plant communities.

Sensitivity and parameter importance

We consider turnover and architecture are considered to be the parameters crucial for determining the species succession. Species from a nutrient-rich successional stage (like *Holcus*) are taller and have a larger SLA, but species from a nutrient-poor habitat (like *Festuca*) are characterized by a slow biomass turnover (Berendse et al. 1992, Elberse & Berendse 1993, Ryser & Lambers 1995). In the nutrient-poor treatment, turnover parameters were decisive for *Anthoxanthum* in competition with *Festuca*, whereas in the nutrient-rich condition, increase in height and SLA increased the competitiveness of *Festuca* in competition with *Anthoxanthum*. In the nutrient-poor condition, however, the SLA appeared to be even more important than the turnover. This is because SLA is an important determinant of the RGR (Poorter & Remkes 1990) that governs the initial growth. This may also have determined the results in the second season of our relatively short experiment. The advantage of turnover is probably more important in the long run.

The sensitivity analysis, however, showed that other important parameters in addition to SLA, biomass turnover and height were parameters considering physiology and allocation. The sensitivity analysis was performed by changing all the parameters by 1%. However, some parameters vary greatly between species whereas others vary little. If the sensitive parameters are considered, parameters determining allocation and physiology show relatively small natural variation (Penning de Vries et al. 1974, Penning de Vries 1975, Poorter et al. 1990, Poorter & Remkes 1990, Poorter & Bergkotte 1992) (magnitude < 50%) whereas our parameterization of the species indicates that shoot turnover, height and SLA were especially highly variable among the species studied (Chapter 3) (magnitude between 200-300%). This suggests that species properties such as SLA, biomass turnover and plant height are much more important in determining the interplant competition and succession than the physiological and allocational properties of the species.

The effect of introducing patchy species distribution

According to the definition of Shipley & Keddy (1994) interspecific competition is asymmetrical when individual plants of the dominating species perform better in the mixed treatment compared to its performance in monoculture whereas at the same time the plants of the subordinate species perform worse than plants growing in monoculture. This means that in

Figure 7 that there must be species above and below the 0.33 line. The deviation from the 0.33 line indicates the degree of asymmetry.

The initial distribution of seedlings affected the outcome of the competition in the spatially explicit simulations. When the mixing of plants of different species was increased, the competitive asymmetry increased in both nitrogen conditions. This is because more patchiness reduces the interaction between plants of different species and increases interactions between plants of the same species (Pacala 1997). This, in principle, leads to slower extinction of patches and might therefore explain the patchiness in real communities.

In the low nitrogen simulations, at the lowest level of mixing, species performed the same as in monoculture, which indicates that the lateral spread of the specie was too small for the species to leave their cells and start interacting with other species. This implies that in principle these species can coexist forever in the model.

In the nitrogen-rich simulations, at the lowest level of mixing, *Holcus* was able to suppress *Anthoxanthum* completely but the growth of *Festuca* was sharply reduced. This indicates that at the high nutrient level the lateral spread of the species was large enough for them to leave their cells and compete with the other two species, which intensified the interaction between superior competitors and subordinate species. Although in real life, vegetation does not grow in cells, plants have a limited zone of influence from which they capture resources. If these resources are limiting in this zone, the lateral spread of individuals is also limited to a level in which they are relatively spatially isolated and there is little competitive interaction between the species (Huston & DeAngelis 1994). This effect can also be observed in our experiment by examining individual plant performance within a pot. In the nutrient-poor treatment, the lateral spread (at the plant base) was not visible at the end of the experiment, whereas in the nutrient-rich treatment, individuals of the superior competitor had spread to cover the soil surface.

However, these results might be an artefact of the relatively low density used in the simulations. This raises the question of whether this effect also holds for other plant densities. The self thinning rule (Yoda et al. 1963) predicts that the number of plants in an area decreases due to interplant competition as the plants grow larger. This means that at a higher nutrient level, larger individuals will occupy more area. This confirms our results and indicates that this process is crucial at various plant densities. The phenomenon of nutrient-poor habitats generally having a higher plant density can be attributed to this process.

In 100% mixed systems (every cell has three species in competition that are well mixed) too, nutrients enhanced competitive asymmetry (Figure 7). In this case the increase of lateral spread cannot explain this effect. The explanation is the difference in nature of light and nutrients. Light is a directional resource, but nutrients are not. This means that bigger plants get disproportionally more light but a proportional amount of nutrients (Weiner 1986), an effect enhanced by the taller stature of many species from nutrient-rich environment (Grime 1979, Elberse & Berendse 1993, Chapter 3).

Both mechanisms described above support the hypothesis put forward by Grime (1973) and Keddy et al. (1997) that predicts that the competitive asymmetry between species increases with the nutrient availability. An increase of competitive asymmetry leads to a quick extinction of species with weaker competitive ability and might be the cause of the smaller biodiversity in nutrient-rich grasslands.

Conclusions

The model's ability to simulate complex perennial competition indicates its potential for analysing complex vegetation processes and succession. The sensitivity of parameters and their magnitude of variation between species (from different fertile environments) confirms the view that plant height, SLA and turnover can be considered as key properties determining competitiveness of species at a certain soil fertility. The simulation results indicate that the winter period favours slow-growing species from nutrient-poor environments because of their slower turnover rate. This enables these species to survive the winter and start growth earlier in spring, giving them a competitive advantage in spring. The spatially explicit simulations showed that patchiness of the species caused a reduction of competitive asymmetry, especially in the nutrient-poor conditions, which indicates that studies of complex vegetation processes should incorporate geographical space.

Appendix A: Temperature dependence of respiration and photosynthesis

Maintenance respiration factor F_m dependent on the average temperature T_a:

$F_m = 0$ if $T_a < 0°C$

$F_m = 0.03333\ T_a$ if $0°C < T_a < 15°C$

$F_m = 2^{((T_a-25)/10)}$ if $T_a > 15°C$

Temperature dependence of the plant growth F_g is dependent on the avarage temperature during the day time T_d.

$F_g = 0$ if $T_d < -5°C$

$F_g = 0.02857\ T_d+0.142$ if $-5°C < T_d < 2°C$

$F_g = 0.1*T_d$ if $2°C < T_d < 10°C$

$F_g = 1$ if $T_d > 10°C$

Appendix B: Calculation of Nitrogen uptake

Nitrogen uptake depends on species demand and the available nitrogen in the soil.

The potential nitrogen uptake (U_p) of a species adapted from Spitters 1989 is:

$U_p = F\ W_{sh}\ (N_x - N_a)$

Where: N_x = the maximum N concentration of the shoot (g g^{-1}), N_a = the actual N concentration of the shoot, W_{sh} is the biomass of the shoot (g DM). F = exchange rate (0.5 d^{-1})

The amount of nitrogen that a species can asses in the soil N_k (g), is related to the proportion of its root length per m^{2}· (or per cell if a spatially explicit version is used).

$N_k = R_k\ /\ (\Sigma\ R_i)$

Where: R_k = root length of species k (m m^{-2}), $\Sigma\ R_i$ = sum of the root length of all species present.

The actual uptake U_a (gN) of species k is in this situation is:

$U_a = \min(\ U_p\ ,\ N_k\ )$

5

Herbaceous plant strategies and coexistence in disturbed habitats

Adapted from: P. Schippers, J.M. van Groenendael, L.M. Vleeshouwers and R. Hunt (submitted)

Abstract

Although many theoretical studies have examined different life history traits of plants, no systematic evaluation has yet been made of the three traits: adult longevity, seed longevity and seed mass, where seed mass is interpreted as being indicative of dispersal distance and seedling vigor. This model study examined the role of these three traits in relation to environmental disturbance. We chose temperate grasslands, widespread in north Western Europe and northern and eastern America, as our reference system for our simulations. Eight plant strategies were defined by permuting two states in each of the three traits taking trade-offs into account. A simple, spatially explicit model was developed to simulate competition among these eight strategies at different levels of disturbance.

Simulations were compared with known disturbance preferences of species similar in strategy in a large database from Sheffield. This showed that some current views on this subject need to be reconsidered. With increasing disturbance level, non-dormant perennials, dormant perennials, non-dormant annuals and dormant annuals respectively predominated, indicating the relative viability of these particular strategies with respect to disturbance.

A new prediction from the model was that stable coexistence occurs between dormant and non-dormant strategies at certain levels of disturbance. Strategies incorporating large seeds were inferior to small-seeded ones if competitive ability of seedlings is proportional to seed weight. This difference was highest at low seed densities and low germination probabilities, indicating that large-seeded species secure no advantage from being dormant (i.e. having a low germination probability). Finally, the results indicated that dormancy is superior to dispersal as a method of coping with disturbance.

Key words: Adult longevity, dormancy, dispersal, establishment, life-history strategies, population dynamics, seed size, seedling vigor, spatially exlicit model

Introduction

In relatively undisturbed habitats, competition between herbaceous species is generally regarded as competition between adult plants and is mediated by their strategies in capturing resources such as light, nutrients and water (Tilman 1982, Berendse 1994). However, when the environment exhibits temporal heterogeneity properties related to demographic processes may become decisive. Disturbance can be regarded as one of the important sources of uncertainty in herbaceous vegetations (Holzapfel et al. 1993, Chambers 1993, Firbank 1993, Bergelson et al. 1993, Huston 1994); Grime (1979) defined it as the removal of plant biomass and considered it, along with environmental stress (in the form of resource- or condition-driven growth limitation) as one of the two most important factors shaping plant evolutionary strategies.

According to the *r*-*K* life history theory of MacArthur (1962) and MacArthur & Wilson (1967), high disturbance levels select for short-lived species with a high population growth rate, that produce many, small, well-dispersed offspring; low disturbance levels would select for competitive, long-lived species with few, large offspring that do not disperse far. For plants, this theory implies that perennials producing few, large seeds with a low dispersal capacity would dominate at low disturbance levels, while annuals with many, well-dispersed, small seeds would dominate at high disturbance levels.

Venable & Lawlor (1980), Levin et al. (1984) and Klinkhamer et al. (1987) considered dispersal and dormancy as alternative methods of dealing with habitat fluctuations. Because wide dispersal is related to low seed mass (Venable & Brown 1988), this view implies that plants adapted to disturbed habitats (i.e., annuals) must either have large, dormant seeds with a low dispersal capacity or small, non-dormant, well-dispersed seeds. As a corollary, we expect non-dormant perennials with large seeds and low dispersal capacity to dominate at low levels of disturbance, while at high levels of disturbance we expect to find annuals either with large, dormant seeds or with small, non-dormant ones.

Results from spatial theoretical studies, however, complicate this view in three ways. First, in several spatial theoretical studies, coexistence was found between superior competitors which nevertheless leave empty spaces in the community when they die and good dispersers which can colonize such spaces rapidly (Fagerström & Ågren 1979, Hastings 1980, Crawley & May 1987, Fagerström 1988, Rees & Long 1992, Tilman 1994). This coexistence indicates that there is no single optimal strategy for any particular disturbance level and that species with contrasting life history strategies might coexist.

This is expected to be true if space becomes available not only through the natural death of large competitors, but also when created by an external disturbance regime. Second, Rees & Westoby (1997) suggested, also from theoretical work, that there might be no single optimal seed mass for any one level of disturbance. A low sensitivity of seed mass in relation to habitat uncertainty appeared to contradict the supposed relation between seed mass and population growth in the work of MacArthur & Wilson (1967). The Rees & Westoby findings, however, could explain the wide variation in seed mass within a single vegetation as (Westoby et al. 1992). Third, Rees (1993, 1994) reported a negative correlation between seed longevity and adult longevity based on a large data set, which suggested that annuals tend to have more dormancy than perennials. This is only partly compatible with the theories of Venable & Lawlor (1980), Levin et al. (1984) and Klinkhamer et al. (1987) who concluded that dispersal can be a satisfactory alternative to dormancy and that well-dispersing annuals should be non-dormant, and vice versa.

These contradictions among the existing theories demand a systematic theoretical investigation in relation to disturbance of the role of three life history traits (adult longevity, seed dormancy and seed mass). The studies mentioned above generally compared only two-strategy mixtures of species in different kind of models (demographical and spatially structured ones) and we believe this approach may be the source of the contradictory results. To avoid these problems, we developed a relatively simple population dynamical model (TRANSPOP) which allowed us to study eight strategies simultaneously, with each strategy being a unique permutation of two levels of each of three life history traits. Strategies were applied to a spatial model at varying levels of external disturbance. The eight different strategies can be considered either as different 'species' or as different sub-populations of a relatively variable species. In the latter context, the results may be evaluated in relation to the Evolutionary Stable Strategy (ESS) approach of Maynard-Smith (1982).

We chose temperate grasslands, widespread in north Western Europe and north and east America, as our reference system for our simulations. We asked: (1) How do various combinations of life history traits (i.e. life history strategies) respond when exposed together to various degrees of disturbance? (2) Do any combinations of life history traits support stable coexistence and, if so, is this dependent on the level of disturbance? Answers to these questions were sought from a simple, spatially explicit model, and the results were compared with the properties of herbaceous species displaying the same life history traits within a comprehensively-studied grassland system in northern England (Grime et al. 1988).

Model description

Spatial structure

To simulate the population dynamics of herbaceous species in the temperate climate zone, a spatially explicit population dynamic model (TRANSPOP) was developed. The model has a spatial structure which is comparable to that used in models by Van Dorp et al. (1997), Moloney & Levin (1996), Lavorel & Chesson (1995) and Crawley & May (1987). Space is represented by a lattice where individual cells represent sites in which plants can establish, die and reproduce. All cells are assumed to have the same properties. As in the models of Lavorel & Chesson (1995) and Crawley & May (1987) the cell size is such that it can accommodate a single adult. This means that the cell size must be related to the plant size of vegetation. Grime (1979) considered a biomass production of 500 g m^{-2} $year^{-1}$ as typical for much of the temperate herbaceous vegetation. Such a vegetation contains about 400 adults (Schippers unpublished results). This translates into an area of 5 x 5 cm for an average adult plant and defines the cell size of the model. In this paper the dynamics of vegetation samples measuring 2 x 2 meters are studied by means of a grid of 40 x 40 cells.

Adult plants produce seeds that are dispersed over the latice. Besides one adult, each cell can contain an unlimited number of seeds of each species present in the vegetation. To avoid edge effects the grid space was modelled as a torus.

Demographic structure

For herbaceous vegetation, the temperate climatic zone is characterized by strongly seasonal changes. At the end of each growing season, most species produce seeds which subsequently disperse. Some seeds germinate in autumn or early spring while others die or stay dormant in the soil. In general, seeds germinate most successfully in vegetation gaps, and seedlings of different species compete for the open site. Open sites are created by external disturbance (sensu Grime 1979) or by the natural mortality of existing adults. Adults may die in late summer or in winter resulting in gaps in autumn or early spring. In this chapter, we simulate the effect of disturbances that happen in spring and summer which thus give rise to a second germination opportunity.

The processes described above form the demographic structure of the model and are summarized in Figure 1 and in Table 1. The state variables are the number of seeds (S), juveniles or seedlings (J) and adults (A) present in each cell. This gives the whole model a simple dynamic structure which is ruled by the seed production per adult F_{as} and by four transition probabilities: (1) the probability that an adult will survive P_{aa}, (2) the probability that a seed will survive P_{ss}, (3) the probability that a seed will germinate and become a seedling P_{sj} and (4) the probability that a juvenile will become an adult P_{ja}. As the number of adults, seedlings or seeds present at any one time in any one cell might be small, all calculations involving numbers and probabilities are done in a demographically stochastic way, resulting in discrete numbers of individuals present in each stage (see Durret & Levins 1994 for mathematical procedure).

In the model one cell can contain only one adult, so a mechanism must be defined to describe the process of adult recruitment P_{ja}. This is usually modelled as a lottery process (Fagerström 1988, Lavorel & Chesson 1995) in which the probability that a seed of a species will become adult is determined by its proportion of germinating seeds.

Because we also incorporated different seed weights into the model, we extended the adult recruitment procedure by introducing a competition factor W which determines the competitive power of the seedling (relative seedling vigor) per weight of germinating seed. For instance, two species will have the same relative seedling vigor (W) when the competitive power of their seedling is proportional to the seed weight.

To simulate the adult recruitment in a cell, first, for each species the number of germinated seeds is calculated:

$$J_i = S_i \cdot Psj_i \qquad \text{equation (1)}$$

With:

S_i = number of seeds of species i in cell (x,y)

Psj_i = probability of seeds of species *i* to germinate and become established as a seedling

Note: this stochastic calculation will result in discrete numbers of seedlings between 0 and S_i.

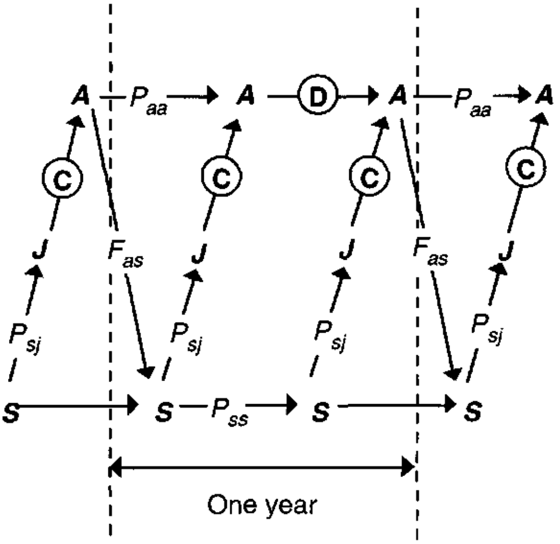

Figure 1. Diagram of life cycle transitions used in the model per year. A = number of adult plants, J = number of seedlings, S = number of seeds. P_{aa}, P_{ss}, P_{sj} are the transition probabilities respectively for adult survival, seed survival and germination. F_{as} = fecundity. C refers to the seedling recruitment process and D to the disturbance process.

Then the probability P_{ja} that a certain species i will become an adult is calculated as:

$$Pja_i = \frac{J_i \cdot W_i \cdot M_i}{\sum_{k=1}^{n} (J_i \cdot W_i \cdot M_i)} \qquad \text{equation (2)}$$

With:

J_i = the number of seedlings of species (i) in a cell

W_i = weighing factor that determines the relative competitive strength of the seedling per seed mass.

M_i = seed mass of a species

n = total number of species in the model (in our case n = 8)

From this probability distribution of all P_{ja} values a species is drawn to take over the cell.

Disturbance

Grime (1979) considered disturbance as 'mechanisms which limit plant biomass by causing its partial or total destruction'. Begon et al. (1990)

Table 1. The sequence of events in a one year cycle of the model (see also Figure 1).

Seq.	Period	Event
1)	Early spring	Germination of seeds
2)	Spring	Mortality of seeds
3)	Summer	Mortality of adult plants by disturbance
4)	Summer	Germination of dormant seeds after disturbance
5)	Autumn	Flowering and dispersal of seeds
6)	Late autumn	Data output presented in the graphs
7)	Winter	Natural mortality of adult plants

redefined disturbance more in terms of population dynamics: 'any relatively discrete event in time that removes organisms and opens up space which can be colonized by individuals of the same or different species'. We will use this latter definition and let disturbance affects adult plant survival. If a cell is disturbed, the established adult dies and there is an opportunity for a new adult to be recruited by germination from the seed bank (Figure 1, Table 1). The level of disturbance was defined as the proportion of cells affected by complete removal of all adult material, and was distributed at random (Table 1, Figure 1).

Definition of strategies

In our approach, we defined eight life history strategies as permutations of two states of each of three life history traits: adult longevity (annual and perennial), seed longevity (dormant and non-dormant) and seed mass (large and small) (Table 2). For each of these traits, trade-offs have to be introduced with respect to other traits not in the model to prevent the construction of a 'Darwinian demon', a species that lives long, produces many large seeds which disperse over a large distance (Rees 1993). These trade-offs concern resource capture and utilization (Harper & Ogden 1970, Gleeson & Tilman 1990).

The trade-off with respect to **adult longevity** can be defined as follows: at one extreme the species can invest mainly in seeds and abandon the mother plant at an early stage (the annual strategy); alternatively, a species can invest mainly in a long-lived and competitive adult plant and produce fewer seeds (the perennial strategy). In consequence, annual species are able to invest

Table 2. Different plant strategies as permutations of adult longevity, seed size and dormancy.

Strategy	Adult longevity	Seed size	Dormancy
ALD	annual	large	dormant
ALN	annual	large	non-dormant
ASD	annual	small	dormant
ASN	annual	small	non-dormant
PLD	perennial	large	dormant
PLN	perennial	large	non-dormant
PSD	perennial	small	dormant
PSN	perennial	small	non-dormant

more in their seeds than perennials. According to Harper (1977), perennial plants invest about 8% of their biomass in seeds, while annuals invest about three times as much. Given the biomass production we have set for the present model (500 g m^{-2}) and the area we have allocated to the average adult plant (5 * 5 cm), the annual productivity was calculated to be 1.25 g biomass (dry matter) per cell. This led to a seed production per cell of 0.1 g for perennials and 0.3 g for annuals assuming that adult plants are of the same size when flowering.

The annual probability of a perennial plant surviving P_{aa} was set at 0.8 after the findings of Antonovics (1972). This means that adult perennials have an average longevity of about 5 years, but that 10% of the plants live for more than 10 years and that 1% survive longer than twenty years.

Individual **seed mass** has a straightforward trade-off against seed number: a plant can invest the permitted fraction of its biomass in many small seeds or in a smaller number of larger seeds (Venable & Brown 1988). This trade-off has three consequences at the population-dynamic level. First, any decrease in seed mass, which allows an increase of number of seeds also results, in the absence of competition, in a higher maximum population growth rate. Second, such a decrease in seed mass reduces the competitive ability of each individual seedling (Spitters & Aerts 1983, Shipley & Keddy 1994). Third, although seed morphology is also an important factor determining seed dispersal (Chapter 6) it is generally assumed that a decrease in seed mass causes an increase in mean dispersal distance (Fenner 1985, Augspurger & Franson 1987, Venable & Brown 1988).

In herbaceous grassland species, the individual seed mass commonly varies within the range 0.1 - 1.0 mg (Grime et al. 1988). We chose these extremes as the weights of our small and large seeds, respectively. Given the level of investment in total seed weight per plant that has already been defined, the tradeoff between seed number and individual weight results in 10 times as many small seeds per plant as large ones. The numerical disadvantage experienced by large-seeded plant is compensated by the ten-fold increase in the absolute vigor of individual seedlings.

Larger seeds clearly disperse over a smaller area. Since the total area available within our model is not very large (2 x 2 meters). Small seeds were allowed to disperse homogeneously over the whole area with an arrival probability in any individual cell of 1/1600, where the distribution of large seeds was restricted to a square of size 55 x 55 cm (i.e. 11 x 11 cells) with the mother plant at the center. To make both dispersal distributions comparable we also set a homogeneous arrival probability for the large seeds at 1/121 per cell. Both arrival probabilities were thus treated in a stochastic way. Since the fecundity F is a large number while the probability for a seed to arrive in a certain cell is small, this resulted in a Poisson distribution for number of seeds per cell.

The trade-offs necessary with respect to **seed longevity** are less clear in physiological terms, since the resources needed for the production of both dormant and non-dormant strategies seem to be the same. However, the trade-off here is well-defined in population dynamic terms: increased dormancy reduces the rate of population growth but enables the species to survive during periods of harsh conditions. Dormant seeds have a second advantage in being able to establish a seed bank which enables them to germinate in other periods of the year, avoiding the competition with non-dormant species which would otherwise occur (Harper 1977, Fenner 1995). This latter property might be very important in explaining the success of dormant strategies in relation to disturbance.

Bakker et al. (1996) distinguished four categories of seed survival in the soil: transient (with a persistence of less than one year), short-term persistent (in the soil for at least one year), persistent (for periods ranging from a few years to a few decades) and long term persistent (for several decades). We chose two contrasting seed bank categories: transient as the non-dormant strategy and persistent as the dormant strategy. For the dormant strategy, the value for annual seed survival P_{ss} was set (like P_{aa}) at 0.8 which implies that seeds have an average longevity of 5 years but that 10% of the seeds live for more than 10 year and that 1% survives even longer than twenty years. Germination probability (P_{sj}) was set at 0.1 (see Table 3). The remaining 10% was seed mortality.

In non-dormant strategies, seed survival P_{ss} was set to zero which means that seeds survive only until the next germination opportunity in autumn or early spring, and then either germinate or die. Seed mortality was kept the same as for the dormant strategies resulting in a germination probability of 0.9 (P_{sj}).

Table 3. Parameterization of different plant strategies (see table 2) in the reference run.

Strategy	P_{ss}	P_{sj}	P_{aa}	F_{as}	Dd (cm)	λ (year^{-1})	M (mg)	W (mg^{-1})
ALD	0.8	0.1	0.0	300	25	3.8	1.0	1.0
ALN	0.0	0.9	0.0	300	25	207.0	1.0	1.0
ASD	0.8	0.1	0.0	3000	100	300.8	0.1	1.0
ASN	0.0	0.9	0.0	3000	100	2700.0	0.1	1.0
PLD	0.8	0.1	0.8	100	25	11.54	1.0	1.0
PLN	0.0	0.9	0.8	100	25	91.59	1.0	1.0
PSD	0.8	0.1	0.8	1000	100	101.59	0.1	1.0
PSN	0.0	0.9	0.8	1000	100	901.60	0.1	1.0

P_{ss} = probability of a seed to survive, P_{aa} = probability of an adult to survive, P_{sj} = probability of a seed to become a seedling, F_{as} = fecundity of the adult, Dd = dispersal distance, λ = the finite rate of increase without density dependence or competition, M = seed mass, W = relative seedling vigor.

Simulation experiments

Reference situation

The parameterization of the eight species as described above is termed the 'reference situation' (Table 3). To evaluate this situation, each simulation started with 200 plants of each of the eight strategies randomly distributed over the whole area of 1600 cells. No seeds were present. The mean number of adult plants per species after 100 years was taken as a practical endpoint for the evaluation. According to Yodzis (1989), species show a stable coexistence if their densities remain positive forever. In this chapter, the mean number of adults per species after 1000 years was considered to be sufficient for evaluating stable coexistence. Reference simulations were performed for a semi-geometric series of disturbance levels: 0, 2, 5, 10, 15, 20, 30, 40, 60, 80 and 95% of the cells affected per year.

Sensitivity analysis of the whole model

To evaluate the effect of parameter choice, the reference situation was compared with simulations in which life history traits were varied individually. This made it possible to determine the importance of life history trait values for each species. The following parameters were varied: (1) perennial plant longevity, (2) seed longevity, (3) dispersal distance of plants with large seeds and (4) seedling competition strength (W) of large seeds. These parameters were varied over five levels each (Table 4). The changes were made only for groups of four strategies at a time (e.g. the four perennials, the four strategies with large seeds) (see Table 4). All other values were kept the same as in the reference situation. The simulations were evaluated for five disturbance levels: 0, 10, 20, 40 and 80%. The mean value and the standard error of three runs after 100 years were taken as a measure for model performance.

Table 4. An overview of the sensitivity analysis. The variation with respect to the reference conditions (bold).

Parameter	Steps				
	-2	-1	0	+1	+2
Perennial plant survival (annual plant survival = 0.0)					
P_{aa}	0.000	0.666	**0.800**	0.857	0.888
Longevity	1.0	3.0	**5**	7	9
Dormant seed survival (non-dormant seed survival = 0.0)					
P_{ss}	0.000	0.666	**0.800**	0.857	0.888
Longevity	1.0	3.0	**5**	7	9
Dispersal distance of large seeds (The dispersal distance of small seeds =100 cm)					
Distance(cm)	5	10	**25**	50	100*
Area (cells)	9	25	**121**	441	1600*
Seedling competition factor W (1/mg) for large seeds (W = 1.0 for small seeds)					
W values	0.6	0.8	**1.0**	1.2	1.4

*Dispersal homogeneous over the whole space.

Sensitivity of germination and establishment processes
To analyse the effect of seed mass on the probability that a species will take over a cell we performed a simulation comprising only the germination and establishment processes used in equations (1) and (2). We calculated the probability that a species with large seeds would take over the cell when competing with a species that has ten times lower individual seed weight when both species have equal amounts of (total) seed weight in the cell. We did this for a series of three germination probabilities (P_{sj}): 0.1, 0.5, 0.9 and at various seed densities.

Simulation results

The results of six single runs under reference conditions indicate that stochastic demographic processes introduce considerable variation in a simulation (Figure 2). Furthermore, under the two extreme disturbance conditions (0% and 80%) only two species completely occupied the site within the space of very few years, while at intermediate disturbance levels more species coexistence occured, sometimes over a very long period (e.g. four species survived to time 500 at disturbance level 5%).

When there was no disturbance the two non-dormant perennial strategies dominated the system together (Figure 3). Increasing the disturbance level to 10% favoured both of the dormant perennial strategies. At a disturbance level of 20%, the four annuals took over. Perennial strategies quickly went extinct above the level of 20% disturbance. This particular level favoured the annuals with non-dormant seeds, but at 40% disturbance, plants with dormant annual strategies became dominant.

All species with large seeds disappeared between 100 and 1000 years of simulation (Figure 3B), leaving only the small seeded ones. However the pattern of dominance of the small seeded species at time 1000 resembles the pattern at time 100 to a large extent. Between the disturbance levels of 2% and 60%, stable coexistence occurred between dormant and non-dormant strategies in both perennial and annual plants. In the very long run, however, no coexistence was found between annual and perennial species.

With an increase in their adult longevity, perennials also increased their competitiveness (Figure 4). As a result, non-dormant annual dominance at the 20% disturbance level disappeared. At disturbance levels of 40% and higher, however, no perennials survived.

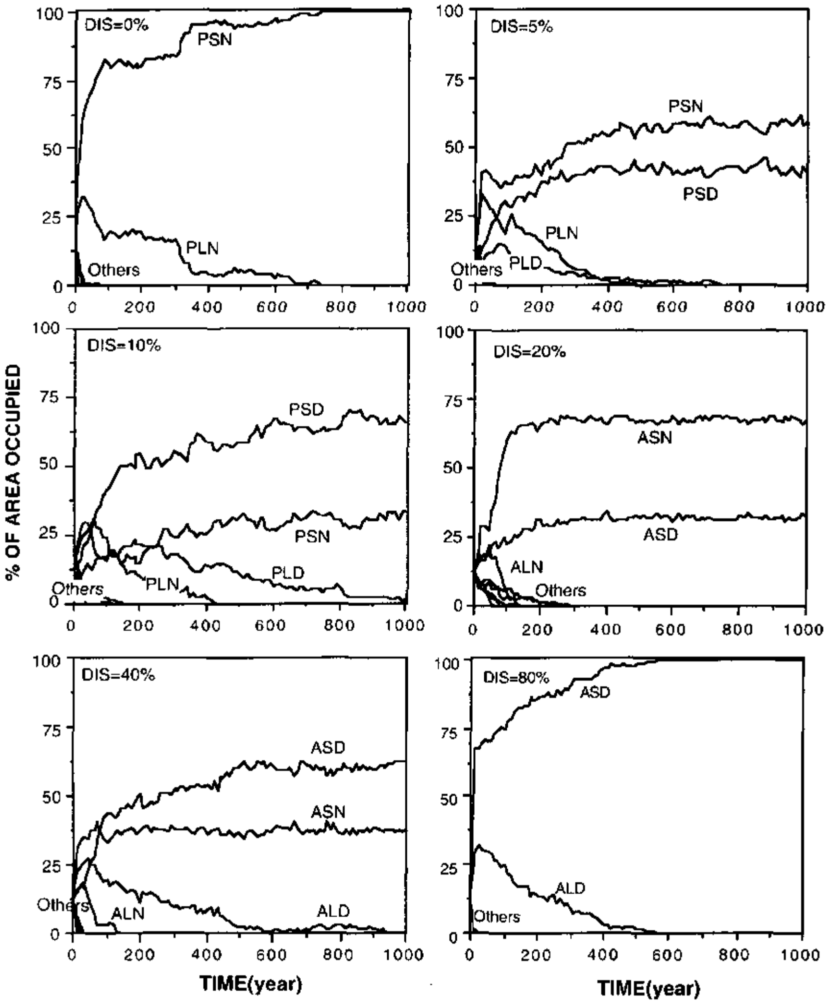

Figure 2. Strategy cover in time at different disturbance levels for the reference conditions. Results of a single simulation in the reference condition. Strategies according to Table 2.

The effect of varying the dormant seed survival parameter had far less effect than changing the adult longevity (Figure 5). When the longevity of dormant seeds was increased there was a sudden jump between years 1 and 3 in the abundance of dormant, small-seeded plants, indicating that some degree of dormancy in well-dispersed plants can favour their competitiveness. With further increases in seed survival, the large-seeded, dormant strategies (with low dispersal) increased, and at all disturbance levels.

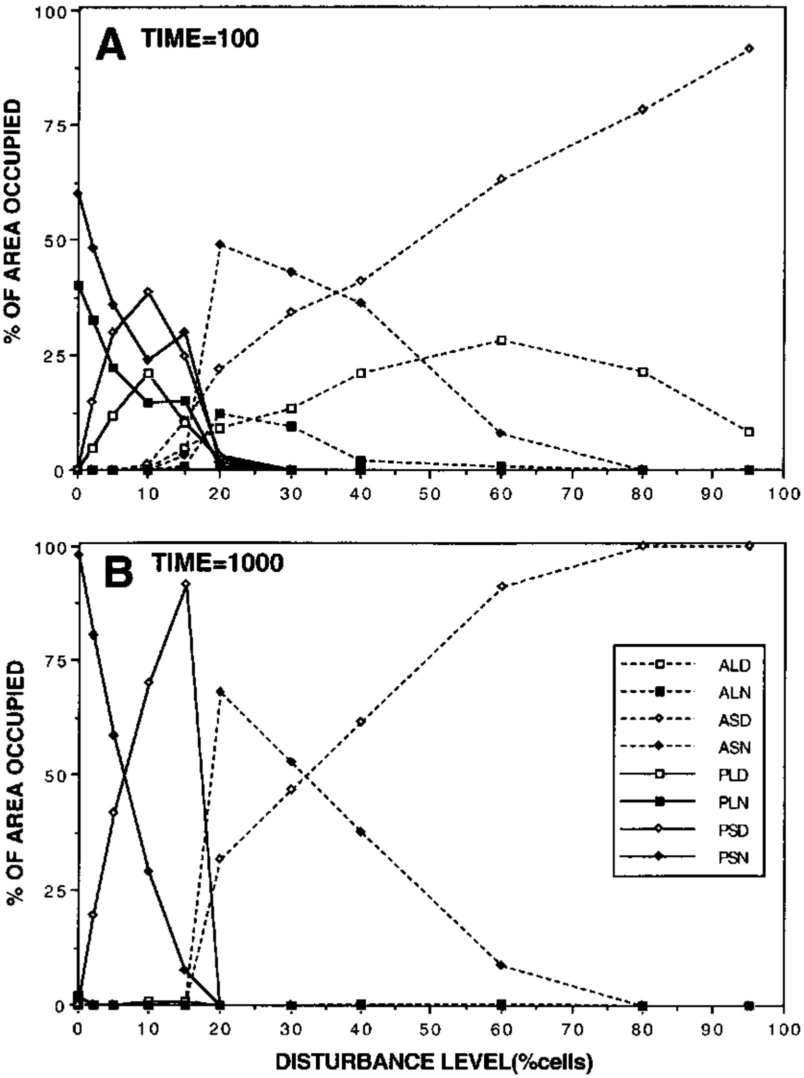

Figure 3. The relation between species cover and disturbance for the reference conditions: after 100 year (**A**), after 1000 year (**B**). Each run started with 200 plants of each of the eight strategies. The points represent the mean value of 6 runs, the maximum SE value in both graphs was 5.1% (N = 6). Plant strategies according to Table 2.

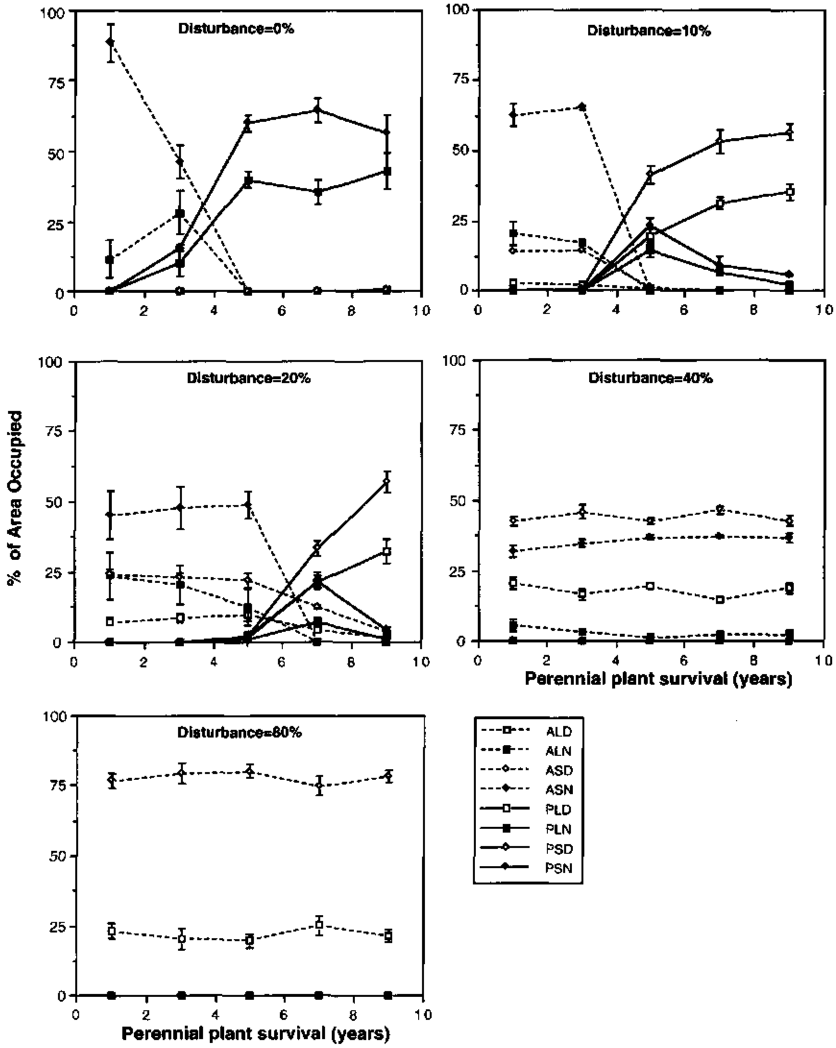

Figure 4. The effect of a change in the perennial plant survival on the percentage of area occupied by the different strategies after 100 years. Each graph represents a different disturbance level. The points represent the mean values of 3 runs, the bars represent ± 1*SE. Plant strategies according to Table 2.

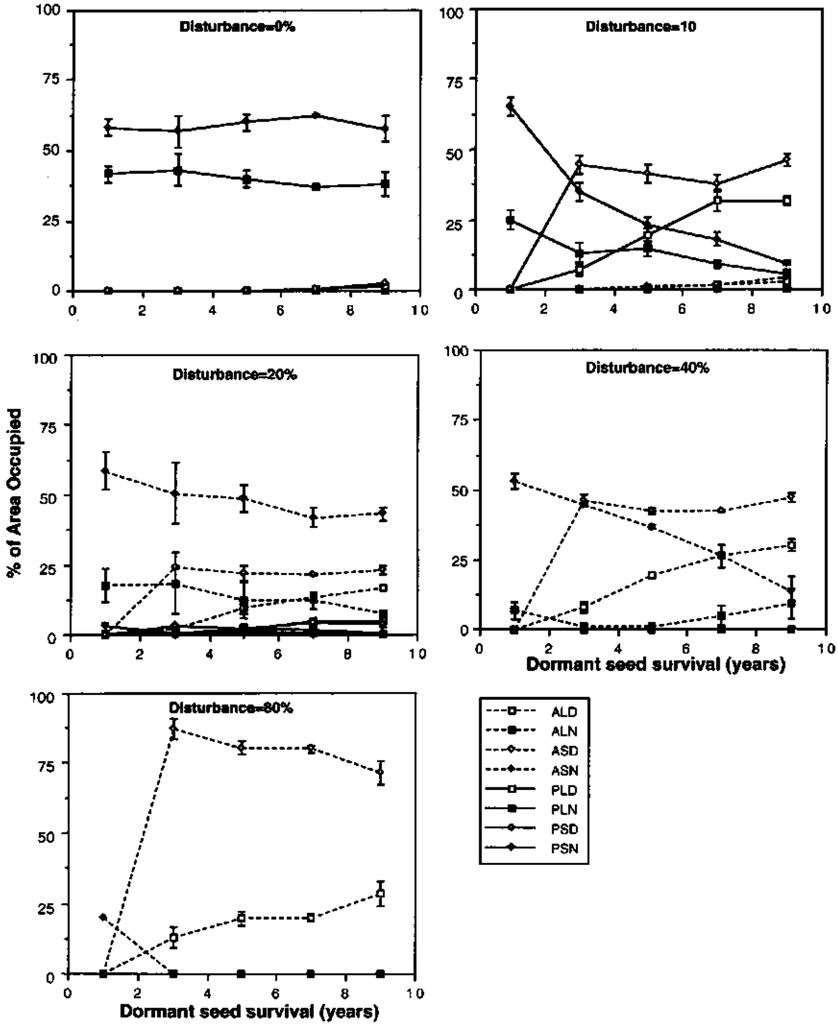

Figure 5. The effect of a change in the dormant seed survival on the percentage of area occupied by the different strategies after 100 years. Each graph represents a different disturbance level. The points represent the mean values of 3 runs, the bars represent ± 1*SE. Plant strategies according to Table 2.

Figure 6 gives the results of varying the dispersal distance. We would expect the same results for both small and large seeds if the dispersal was homogeneous over the 1600 cells (dispersal distance = 100 cm). However, results indicates that, if strategies (with high and low seed mass) were dispersed homogeneously, strategies with a low seed mass were superior at all disturbance levels due to their numerical superiority (Figure 6). Remarkably, large-seeded species were very sensitive to small variations in dispersal around the mother plant. Increasing dispersal from 5 to 25 cm from the mother cell could to a large extent secure the capacity of large seeded species to maintain themselves.

Of all traits analysed, varying seedling vigor had the most dramatic effect. The general balance of disturbance-related dominance between annuals and perennials was maintained, but small changes in seedling vigor could completely reversed the ranking of small- and large-seeded species (Figure 7). The graphs are quite symmetrical, but the point of symmetry is not 1.0 (i.e. the reference situation) but is shifted to the right. This indicates that strategies with small seeds were superior when the relative seedling vigor of small and large seeded plants was the same.

Simulations of the effect of seed mass on germination and establishment in a vegetation gap (Figure 8) indicate that small seeds are always better competitors than large seeds when the biomass of the sum of al the seeds was the same and the seedling vigor was proportional to the seed weight. This effect increased strongly when low numbers of seeds were involved at low germination levels.

Comparison with a real flora

To compare the eight combinations of traits used in the model with similar combinations in real plants, herbaceous plants of the extensive Sheffield data set (Grime et al. 1988) were classified according to the model life-history traits. The distributions of eight groups of real species were examined in relation to the abundance of bare soil in the field records and the mean position of the group in the R-dimension of C-S-R space (Grime 1974, 1977, 1979) both of which are strongly related to disturbance level (Grime et al. 1988, Grime et al. 1997).

First, the Sheffield species were assigned to the different strategies in the following way: seeds larger than 0.5 mg were classified as large seeds and seeds smaller than 0.5 mg were classified as small seeds, seeds that live

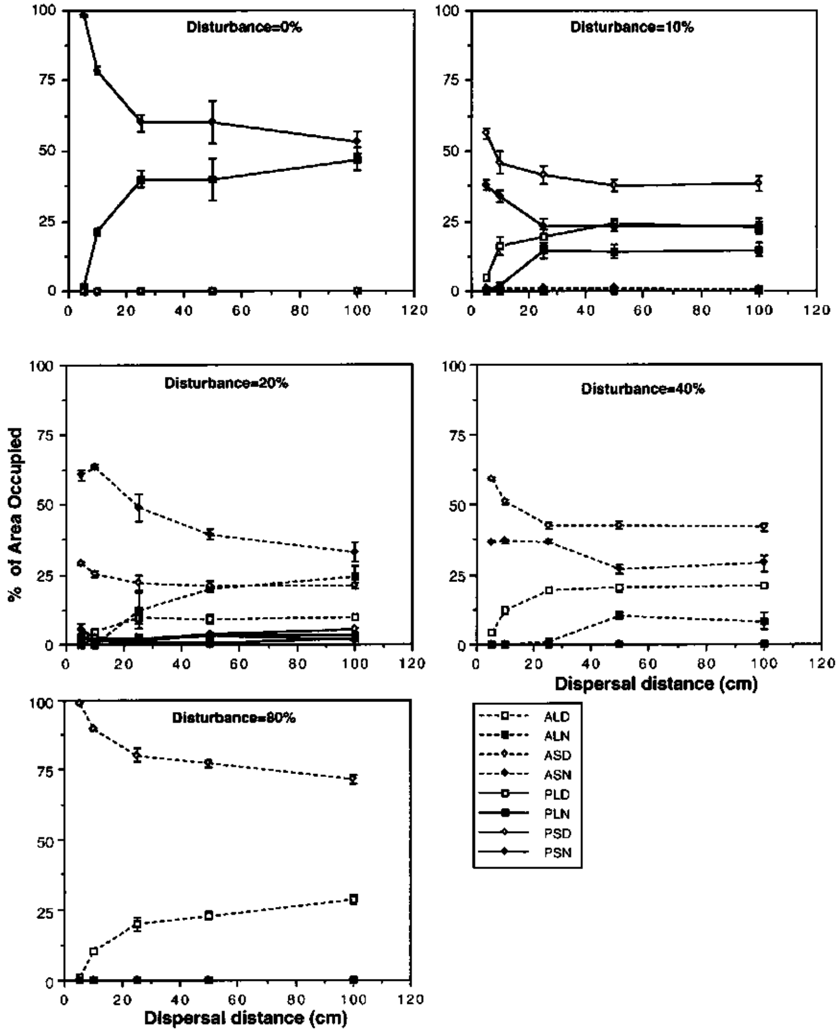

Figure 6. The effect of a change in the dispersal distance of the large seeds on the percentage of area occupied by the different strategies at after 100 years. Each graph represents a different disturbance level. The points represent the mean values of 3 runs, the bars represent ± 1*SE. Plant strategies according to Table 2.

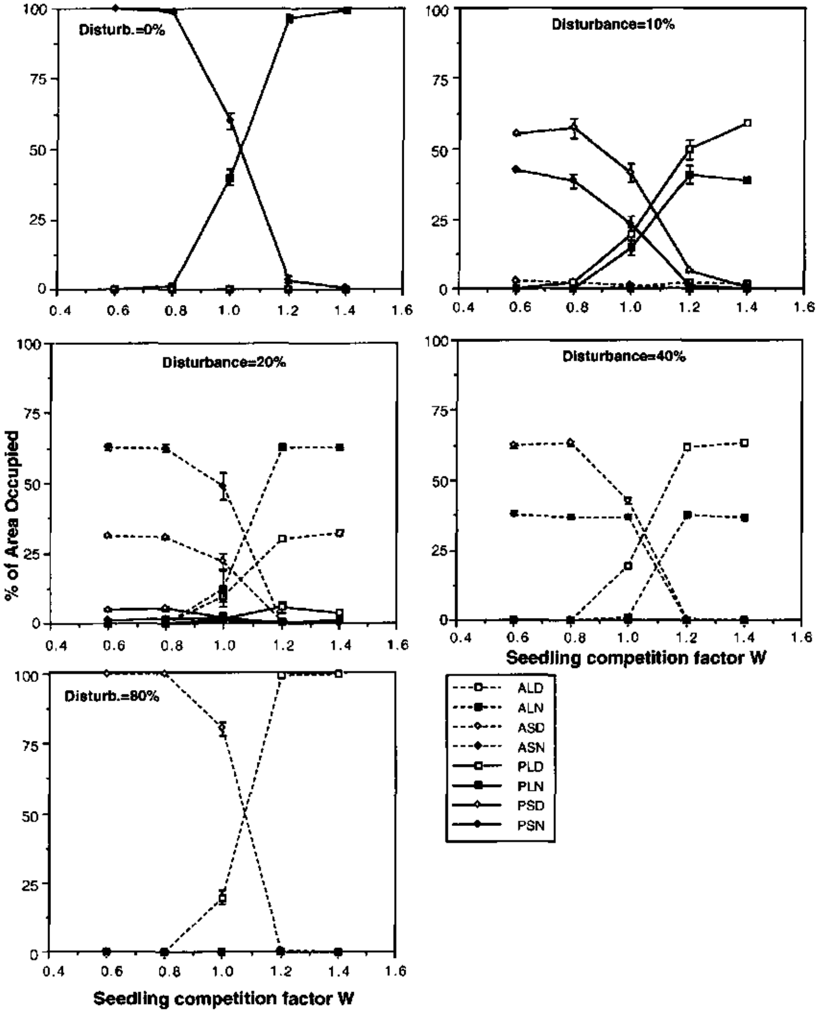

Figure 7. The effect of a change in relative seedling vigor W per seed mass (1/mg) of the large seeded strategies on the percentage of area occupied by the different strategies after 100 years. The competing strategies with small seeds are 10 times smaller but have a seedling vigor of 1.0. Each graph represents a different disturbance level. The points represent the mean values of 3 runs, the bars represent ± 1*SE. Plant strategies according to Table 2.

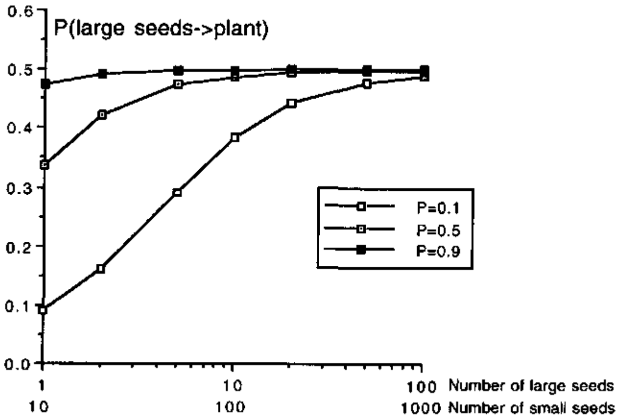

Figure 8. The probability that a species with large seeds will take over a cell (gap) when it competes with a species with 10 times smaller seeds that have the same relative seedling vigor (1/mg) (seedling competitiver strength per g seed). Note that along the X-axis the total seed biomass of both species is the same.

shorter than one year were classified as non-dormant whereas seeds with a persistent seed bank were classified as dormant, adult longevity (annuals and perennials) were classified as in the data base. The dormancy classification of Thompson et al. (1997) was used to fill gaps in the Grime database. Perennials with extensive clonal growth were classified separately.

Second, for each species the distribution of preferences among the bare soil categories (Grime et al. 1988) was standardized to 100%. The mean preference of all species belonging to each strategy was calculated as a measure of its bare soil (or disturbance) preference.

The R axis of the C-S-R system of plant functional types (Grime 1979) is a measure of the extent to which the species is adapted to productive, disturbed conditions. High relative growth rate, low stature and lateral spread, and high reproductive capacity are properties of such species and can together be regarded as indicators of disturbance-adaptedness (Grime et al. 1997). A mean R-coordinate can be calculated on a scale of +2 (most like the pure R-type) to –2 (least like this type). The mean value of this coordinate within each of the eight groups of species can be regarded as a measure of adaptation to disturbance.

The results of the classification of Sheffield species are shown in Table 5. Noticeable was the low representation of annuals with non-dormant seeds. Further, dormancy occurred more often in small-seeded species than in large-seeded ones. The perennials had a general preference for between 0% and 25% bare soil in the field records, with the exception of the dormant type with small seeds (PSD) which ranged between 10% and 50% bare soil. Both the dormant, annual strategies clearly preferred the highest of the bare soil categories (above 75%). Non-dormant annuals with large seeds preferred categories above 50% while non-dormant annuals with small seeds had a greatest preference between 26 and 50% bare soil (note that this category consisted of two species only). Clonal perennials showed in general little preference.

The mean R-coordinates indicate that non-clonal perennials are in general not well adapted to disturbance (all of the values are negative, indicating that they occupy below-average positions on the disturbance scale within C-S-R space). Within the annual groups, non-dormant species are moderately adapted to disturbance (with neutral R-coordinates) while dormant annuals are highly adapted to disturbance (with strongly positive coordinates). The sizeable group of clonal perennials is also moderately adapted to disturbance.

Table 5. Frequency distribution of herbaceous plant strategies over bare soil categories and the standardized R axis value (a measure for the disturbance preference of the species) of different live history strategies classified according to adult longevity, seed mass and seed bank characteristics. Strategy definition according to Table 2. Analyses is based upon 252 common plants in the Sheffield area (Grime et al. 1988).

Strategy	PLN	PSN	PLD	PSD	ALN	ASN	ALD	ASD	CLONAL
Percentage	20.2	5.2	8.3	15.7	3.2	1.1	5.6	12.3	32.7
Bare soil preference									
0-10%	**24.3**	**26.6**	**27.0**	19.5	17.4	7.1	5.4	9.7	24.7
10-25%	**26.8**	**33.4**	**38.8**	**25.7**	13.1	8.9	9.6	13.2	22.3
26-50%	23.0	21.4	8.8	**28.8**	14.0	**66.1**	11.8	12.6	17.45
51-75%	17.8	15.2	16.3	17.7	**27.7**	17.9	6.6	18.6	21.73
76-100%	8.1	3.4	9.1	8.3	**27.8**	0.0	**66.6**	**45.9**	13.9
R coordinate *)									
Percentage (n=362)	18.2	6.3	9.4	12.9	2.4	1.3	7.4	12.4	29.8
Mean R coord.*	-0.58	-0.35	-0.65	-0.43	0.56	0.0	1.52	1.11	-0.54

*) R coordinate: 0 = average, >0 prefer disturbed habitats, <0 avoid disturbed habitats)

Discussion

When performing any model study it is important to bear in mind the assumptions that have been made. Here, the two major simplifications are that neither competition between adult plants of contrasting strategies nor clonal spread have been incorporated. This limits the validity of the model to vegetation types which are not dominated by clonal species and that there are limited diffences in the adult competitiveness among species. On the other hand, the incorporation of both these missing processes would have increased species numbers and model complexity considerably, raising further difficulties with interpretation of the results.

The present results can also be evaluated from the point of view of the ESS (evolutionary stable strategies). This is achieved by asking questions such as 'In what way should a relatively sessile plant species invest its limiting resources when exposed to a certain level of disturbance and when in competition with other individuals of the same species?'. In this respect, the different strategies can be regarded as mutants of one other with respect to the three traits studied here if their other attributes, including adult competitiveness, are assumed to be the same. We believe that both the evolutionary and the vegetation-science approach to the interpretation of these results will, in general, lead to comparable conclusions about the fitness of the various trait combinations in the real world.

Adult longevity

The results of our simulations indicate that there is a clear range within our environmental disturbance scale in which perennials exclude annuals (0-20%) and also a range where annuals exclude perennials (20-100%). The necessary trade-off between the annual and the perennial habit is the longer lifespan of the perennial versus the higher seed production of the annual. The clear segregation of perennials and annuals by disturbance can therefore be explained by the fact that disturbance only affects the adults but not the seeds. Above a certain risk level, which in our model is at about 20% disturbance, investment in seeds is more profitable than investment in the adult longevity. This allows annuals to exclude their perennial counterparts above this level.

Results from the Sheffield database agree with the simulations. Sessile perennials showed more preference for low bare soil categories while annuals prefer an environment with higher levels of bare soil. Furthermore the R-coordinates, as measures of environmental disturbance in the field, differed strongly between perennials and annuals. Annuals have neutral to highly positive R values whereas perennials have uniformly negative which indicate that annuals are more adapted to higher levels of disturbance and perennials are not (Grime et al. 1997). These results agree with experimental results of Wilson & Tilman (1991) and in principle support the *r-K* life history concept of MacArthur (1962) and MacArthur & Wilson (1967) which predicts that long-lived species are superior competitors at low disturbance levels while short-lived species with high numbers of offspring are superior at higher levels of disturbance.

Seed longevity

Our simulation results indicated that an increase in disturbance frequency changes the ratio between strategies, with short-lived seeds giving way to long lived ones. This occurred within both annual- and perennial-dominated disturbance ranges. A second important result of the simulations is that dormant and non-dormant species can coexist over a large range of disturbance levels. These results can be explained by the fact that there are two germination opportunities within the model. Vegetation gaps are created by natural adult mortality during winter and become potential germination sites in spring. Short-lived seeds with high germination probabilities were particularly successful in taking over these gaps because of their numerical superiority. Later in the season, a second germination opportunity can be created by disturbance. Since short-lived seeds do not survive to this second opportunity, the long-lived seeds have an opportunity to establish in the absence of competition from species with short-lived seeds. This second germination opportunity can be considered as a population regeneration niche (Grubb 1977) for species with dormant seeds. From these disturbed spots, the dormant plants can build up a seed bank that subsequently increases their chance of establishment in the next season's first germination period.

Coexistence of types occurred in our model because only a fraction of the cells was disturbed on any one occasion. In these disturbed cells, dormant strategies established while in the other cells mainly non-dormant strategies established. Coexistence between dormant and non-dormant strategies has not been reported before and can be considered as a new mechanism for the explanation of species coexistence.

With an increase in disturbance, the simulation results predict a general domination sequence which comprises non-dormant perennials, dormant perennials, non-dormant annuals and dormant annuals. Since the field measures of bare soil percentages and the R-coordinate values are supposed to be positively correlated with the disturbance level we should be able to expect the same sequence within the Sheffield data base analysis. Although the results within the perennial group were less clear, the results of Table 5 confirm this expectation. The results within the perennial group were less clear possibly due to the narrow range of disturbance levels where perennials dominate. This makes it difficult for the relatively rough database-analysis to determine the dominance of dormant and non-dormant perennial strategies, that even might coexist, in this small range.

Seed mass

Our simulation results demonstrated that seed mass showed no strong relation to the level of disturbance, in contrast with the other two traits. In the long run, all species with large seeds were outcompeted by their counterparts with small seeds. This difference was partly due to the better dispersal capacity of species with small seeds. Better dispersal leads to a more homogeneous spread of seeds in space, decreases the probability of intraspecific competition, and increases the competitive ability of a species, as shown by our sensitivity analysis (Figure 6). However, differences other than the larger dispersal capacity of small seeds are important, because the sensitivity analysis showed that large seeds still perform worse even when their dispersal capacity matches that of small seeds. The reason for this is to be found in equations (1) and (2). These simple equations behave differently when probability processes are calculated in a stochastic way, as shown by the simulation results (Figure 8). In general, this will lead towards selection for smaller and smaller seeds if the relative seedling vigor does not vary with seedmass.

However, sensitivity analysis showed that varying the relative seedling vigor of large seeds had a greater impact than changing any of the other life history traits (Figure 7). A complete dominance by small-seeded species gave way to a complete supremacy of larger-seeded species when the value of relative seedling vigor (W) of large seeds was increased from 0.8 to 1.2 (small seeds had $W = 1.0$). In practical terms, this implies that plant species should optimize their seed mass for maximum relative seedling vigor. This maximum vigor, in turn, is dependent on plant growth properties and strategy of regeneration. This may explain the high variability of seed mass observed between species that grow in a single vegetation (Westoby et al. 1992).

Seed longevity and adult longevity

Rees (1993, 1994) stated that annuals should have seed dormancy to cope with habitat uncertainty. The simulations, however, indicate that non-dormant annuals exhibit a viable strategy at intermediate levels of disturbance. The low abundance of non dormant annuals in the Sheffield database seem to support the view of Rees. But these results may as weel be cause by the low abundance of intermediate disturbance in the Sheffield region (Grime et al. 1988).

The contrast between the results of Rees' model and ours can be explained by the difference in the method of application of disturbance. Rees used a factor that ruled fecundity and let it vary between 0.0 and 1.0 with a probability of 0.5. This caused, on average, a total failure of reproduction once every two years. It is clear that non-dormant annuals would not survive such a failure and therefore were not successful in Rees' model. In our model, disturbance was varied as a percentage of cells affected every year; this caused reproductive failure in only a part of the population, the remainder of which could still reproduce. In our view, the habitat uncertainty, which was defined by Rees, is too extreme and might only be valid in some special agricultural situations. This leads to the conclusion that non-dormant annual strategies are a viable at intermediate disturbance levels.

Seed longevity and seed mass

We have already mentioned the stochastic advantage of smaller seeds, as demonstrated by Figure 8. The same figure indicates that the difference between large- and small-seeded strategies increased at low germination probability P_{sj} and at low seed numbers. This implies that strategies with large seeds should avoid being dormant (i.e. having a low germination probability) when low seed numbers are involved. This simple theory may explain the fact that large seeds avoid dormancy more often than small ones, as reported by Venable & Brown (1988) and Thompson et al. (1993). The frequency distribution of dormant and non-dormant strategies over the seed mass categories in the Sheffield data base confirms this expectation; large seeds were more than twice as often non-dormant than dormant, while small seeds were more frequently dormant.

Dispersal and dormancy

One of the two major consequences of seed mass is that small seeds have a better dispersal capacity. Venable & Lawlor (1980), Levin et al. (1984) and Klinkhamer et al. (1987), defined dormancy and dispersal as alternative ways of coping with disturbance. Our sensitivity analysis showed that when the seed longevity of the dormant seeds was increased, large seeds with low dispersal capacity profited more than strategies with small, well-dispersed seeds. Confirming this theory, Rees (1996) also reported lack of dormancy in large seeds with good dispersal properties. Although this information suggests that dormancy and dispersal are alternative ways of dealing with disturbance, we did not find non-dormant annuals with well dispersed, small seeds dominating at high disturbance levels in the simulations. Results from the Sheffield data set confirm this view; dormant annuals are associated with the highest disturbance indicators and often have (large) seeds with low dispersibility. This contradicts the theory that dispersability is a good alternative for dormancy; dormancy might be a better way of coping with disturbance than dispersal.

Conclusions

In this chapter, we studied the effect of disturbance on vegetations in temperate climatic region by means of a relatively simple, population-dynamical model. From our initial assumptions, we are satisfied that increasing disturbance creates a sequence in the predomination of non-dormant perennials, dormant perennials, non-dormant annuals and dormant annuals. The model also predicts that dormant and non dormant strategies may coexist at various levels of disturbance.

When seeds are abundant, species should optimize the seed mass to maximize the realtive competitive ability (W) of their seeds. The higher preference of larger seeds for the non-dormant habit might be explained by stochastic theory that predicts a strong disadvantage for large, dormant seeds when competing at low numbers with smaller seeds. Finally, we conclude from our simulation results and database analyses that dormancy is a better way to cope with disturbance than dispersal, i.e. that escape in time is more important than escape in space.

6

Modelling seed dispersal by wind in herbaceous species

Adapted from: E. Jongejans & P. Schippers. 1999. Oikos 87: 362-372.

Abstract

Wind can be regarded as the most important vector in seed dispersal in open grassland vegetations. Experimental estimations of seed dispersal distances in this environment are complex because of low arrival probabilities at large distances. Therefore, a proper mathematical generalization would be essential to give insight in dispersal probability distributions. Hence a promising individual-based model for seed dispersal presented by Andersen (1991) was tested for different wind velocities and seeds. Simulation results from the seed dispersal model were compared with observations in a horizontal wind tunnel. Considering the large variation in seed morphology and mass, the simulation results fitted wind tunnel results reasonably well, indicating the general applicability of the tested model for herbaceous species. Model sensitivity was evaluated with respect to wind speed and vegetation height. Differences in wind speed had a larger impact on the tail of the seed shadow than on median dispersal. However, vegetation height had little impact on the tail of the seed shadow compared to the median.

Terminal velocity (V_t) is the crucial species specific parameter in wind dispersal models. There are two frequently used methods to determine V_t: a dropping method and a method to float seeds in an upward air stream. However, these methods have never been compared directly. This paper presents V_t-values determined with both methods. In general results were in the same order. Only for high values of V_t the results of the floating method were found to be lower than the results of the dropping method. Simulation results showed that the intraspecific differences in V_t-values were an important factor in determining the seed shadow.

Key words: Dispersal distance, model, seed shadow, terminal velocity, turbulence, wind tunnel, wind speed.

Introduction

Seed dispersal can be regarded as a key process in survival and distribution of plant species (Primack & Miao 1992, Venable & Brown 1993, Quinn et al. 1994, Begon et al. 1990). Seeds are dispersed in many different ways: by wind, water, ballistic mechanisms, animals. In open grasslands, however, wind can be regarded as one of the most important vectors (Ridley 1930, Van der Pijl 1982). The dispersal distances of all seeds of a certain plant displaced by the wind form a seed shadow, a probability density curve of arrival probabilities (Willson 1993). For an estimation of the recolonization rate the tail of this seed shadow, representing the furthest blown seeds, can be regarded as at least as important as the median (Portnoy & Willson 1993, Van Dorp et al. 1997).

It is difficult to estimate seed shadows of wind dispersal experimentally because the tail of these functions is characterized by very low probabilities. This problem could be overcome with good explanatory models to describe the wind dispersal process. Two kinds of mechanistic seed shadow models have been described (Greene & Johnson 1989, Okubo & Levin 1989, Andersen 1991): (1) Seedflux models, that describe seed densities in x,z space analytically and (2) individual-based models, that simulate the flight of one seed in time and produce seed-shadow curves by combining many simulated dispersal distances. In both models the displacement rate of the seed in horizontal direction equals the wind speed and is determined by the terminal velocity in vertical direction. Terminal velocity is the speed finally reached when a seed is falling in motionless air (Verkaar et al. 1983). Gaussian functions describe air turbulence in these models.

An advantage of individual-based models is the possibility to add extra processes like vegetation-roughness dependent wind profiles. Furthermore, Andersen (1991) showed that an individual-based model gives better results than seedflux models when predicting seed-shadow curves. Although Andersen's individual-based model is promising it has only been tested for plumed seeds of one species using mean terminal velocity.

The most important species specific characteristic used in dispersal models is terminal velocity (V_t). Terminal velocity is determined by seed morphology and -weight, and can be obtained by two methods (Browder & Schroeder 1980): (1) A dropping method, using a fall tower in which seeds are dropped from a certain height in motionless air (Schulz et al. 1991, Greene & Johnson 1993, Askew et al. 1997) and (2) a floating method, using a vertical wind tunnel in which seeds float and the necessary upward air flow is determined (Bilanski & Lal 1965, Law & Collier 1973, Hofstee 1992). The advantage of the floating method compared to the dropping method is that the terminal velocity can be obtained directly and that the apparatus can be relatively small. A disadvantage is that it is difficult to obtain a smooth air flow with little turbulence. Although both methods were used in the past, a good comparison between the two has never been made.

A promising seed-shadow model found in literature is Andersen's individual-based model incorporating turbulence. However, this model has not been tested for more than one species with plumed seeds. Therefore our first objective is to test the generality of this model for various herbaceous seeds that differ with respect to seed weight and the presence of plumes. Furthermore our aim was to test model sensitivity with respect to wind speed, vegetation height and intraspecific terminal velocity range.

Terminal velocity can be regarded as the most important species specific model parameter for determining the seed shadow caused by wind. Two methods have been used to obtain V_t. However, a good comparison between the two methods for estimating terminal velocities has never been made. Therefore, the second objective of this paper is to evaluate these methods.

Methods

Terminal velocity measurements: Dropping method

For the terminal velocity measurements 21 grassland species (collected in The Netherlands) were chosen (Table 1). Seeds were released in a fall tower consisting of a square tube of 42 by 42 cm in a stairwell, and had a free fall over a height of 15.83 m. The time needed for this fall was measured electronically by use of a photo sensor just below the point of release and by a piezo element (which senses vibrations) in the plate on which the seeds landed (Hofstee 1992, Grift et al. 1997). For seeds with a low rate of descent and thus too little impulse to trigger the piezo element, the time was stopped manually, and corrected for the reaction time of the observer. For each species the falling time was thus measured for 20 randomly selected seeds. The terminal velocity was calculated by dividing the height of the fall tower by the duration of the fall, with a correction for the acceleration process. For *Crepis capillaris* (L.) Wallr. and *Hypochaeris radicata* L. no measurements were made because seeds were not collected at the time.

Table 1. Mean terminal verlocity measurements and weight of seeds used (n=20). The the range indicates minimum and maximum values of 20 seeds.

Species	Morphology	Weight	Terminal velocity	
		[mg]	Dropping method [ms^{-1}] mean (range)	Floating method [ms^{-1}] mean(range)
Species used for the model evaluation				
Crepis capillaris	plume	0.09		0.42 (0.21 - 1.05)
Picris hieracioides	plume	1.11	0.83 (0.27 - 1.79)	0.65 (0.28 - 1.34)
Leucanthemum vulgare	cylinder	0.39	2.62 (1.84 - 3.26)	2.63 (1.96 - 3.05)
Silene latifolia subsp. *alba*	ball	1.04	4.35 (3.30 - 5.04)	3.92 (3.38 - 4.39)
Species used for measurements				
Taraxacum officinale	plume	0.78	0.43 (0.36 - 0.54)	0.34 (0.13 - 0.49)
Hypochaeris radicata	plume	1.05		0.54 (0.30 - 0.97)
Holcus lanatus	caryopsis/lemma	0.22	0.84 (0.63 - 2.02)	0.91 (0.60 - 1.70)
Linaria vulgaris	winged disk	0.15	0.92 (0.47 - 1.19)	0.95 (0.70 - 115)
Hieracium pilosella	plume	0.17	0.98 (0.36 - 1.81)	0.71 (0.23 - 1.14)
Tanacetum vulgare	cylinder	0.12	1.04 (0.67 - 2.06)	1.06 (0.71 - 1.51)
Leontodon autumnalis	plume	0.66	1.33 (0.43 - 3.20)	1.13 (0.69 - 2.15)
Campanula rotundifolia	ball	0.07	1.53 (1.24 - 1.78)	
Festuca ovina	caryopsis/lemma	0.31	1.62 (0.80 - 2.66)	1.98 (1.31 - 2.39)
Anthoxanthum odaratum	caryopsis/lemma	0.58	1.86 (1.02 - 2.99)	1.61 (1.00 - 2.15)
Daucus carota	cylinder	0.85	2.01 (1.38 - 3.41)	1.71 (0.97 - 2.96)
Poa annua	caryopsis/lemma	0.45	2.34 (1.81 - 2.95)	2.45 (1.79 - 3.31)
Chenopodium album	ball in capsule	0.78	2.71 (1.55 - 3.90)	2.56 (1.58 - 3.08)
Rumex obtusifolius	ball/perianth	3.19	2.72 (1.71 - 3.57)	2.53 (2.10 - 2.88)
Plantago lanceolata	cylinders in caps.	2.92	3.41 (1.44 - 4.95)	3.08 (1.65 - 4.60)
Galium mollugo	ball	0.62	3.62 (2.19 - 4.32)	3.35 (2.79 - 4.36)
Centaurea jacea	cylinder	2.06	4.13 (3.32 - 4.79)	3.41 (2.57 - 3.93)

Terminal velocity measurements: Floating method

A vertical wind tunnel (Figure 1) was constructed using a transparent tube of 5.2 cm diameter. A fan caused an upward airflow, which was stabilized by a box in which the flow rate was very low, resulting in an even distribution of the underpressure over the cross-section of the tube. Underneath the tube, where the air was sucked in, a funnel with a grid was placed to minimize air turbulence. The grid, 7 cm high, consisted of adjoining holes with a diameter of 6 mm.

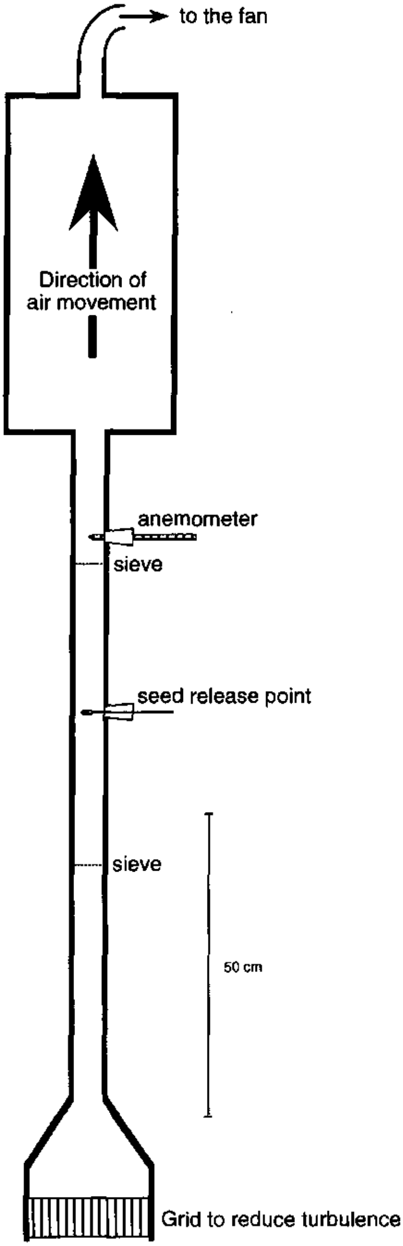

Figure 1. A vertical section of the used vertical wind tunnel.

In the tube a section of 50 cm was enclosed by 2 sieves in which the seeds were released. The flat metal sieves, necessary not to lose the selected seed, had openings with a diameter of 0.7 mm. The flow rate was measured with a hot-wire anemometer. The measurements 7.4 cm above the upper grid (to keep from disturbing the air flow in the section), were adjusted for the small difference in measured flow rates above and in the section.

Seeds were released through a hole in the measuring section of the tube, which was closed again immediately. The flow rate was recorded at which a seed floated in the middle of the section. *Campanula rotundifolia* L. seeds were too small as they were able to penetrate the sieves of the vertical wind tunnel making measurements impossible. Seeds used in this methods were randomly selected from the same seed population as for the dropping method.

Model and test

A stochastic model incorporating turbulence was constructed according to Andersen (1991). The model calculated the flight of an individual seed from the seed source at a height z in a x, z space until it reached the ground. A seed shadow was obtained by adding the arrival distances of many simulations. The mean process, the velocities in downwind (X) and vertical (Z) direction, is described by:

$$\frac{dZ}{dt} = -V_t \qquad \text{equation (1a)}$$

$$\frac{dX}{dt} = u_w \qquad \text{equation (1b)}$$

in which u_w is the strength of the wind at height Z. If there is a homogenous wind profile (the wind speed is equally strong at all heights), a seed will fall with velocity V_t and move a distance of $u_w * Z / V_t$ in X direction (Matlack 1987, Ernst et al. 1992; Greene and Johnson, 1992). Above a vegetation a logarithmic profile is a more realistic distribution of wind speeds over height. When there is no thermic updraft the wind speed at a certain height is (Goudriaan 1977, Okubo 1980, Monteith & Unsworth 1990):

$$u_w = \left(\frac{u_*}{k}\right) \cdot \log\left(\frac{(Z - d)}{z_0}\right) \qquad \text{for } Z \geq d + z_0 \qquad \text{equation (2a)}$$

$$u_w = 0 \qquad \text{for } Z < d + z_0 \qquad \text{equation (2b)}$$

in which u_* is the friction velocity, k the Von Karman constant (0,41), z_0 a measure for the roughness of the vegetation and $d + z_0$ the height at which the wind speed is zero. The effect of turbulence on vertical seed flight can be seen as an additional, stochastic process affecting vertical seed position. This was modeled by considering the distance of falling as caused by Brownian motion with mean $M = - V_t$ and variance $V = k\ u_*\ Z\ t$. Andersen (1991) used the generalized derivative of this Brownian motion, Gaussian white noise (W), to obtain a stochastic differential equation describing the change in vertical seed position in time. This equation was described in Andersen's (1991) article as:

$$\mathrm{d}Z = 1/2(k \cdot u_* \cdot t - V_t)\mathrm{d}t + (2 \cdot k \cdot u_* \cdot Z \cdot t)^{1/2}\mathrm{d}W \qquad \text{equation (3a)}$$

However, this equation included a misprinted bracket, and should be:

$$\mathrm{d}Z = (1/2 \cdot k \cdot u_* \cdot t - V_t)\mathrm{d}t + (2 \cdot k \cdot u_* \cdot Z \cdot t)^{1/2}\mathrm{d}W \qquad \text{equation (3b)}$$

The ($1/2\ k\ u_*\ t$)-part (Gardiner 1990) may be neglected because it was very small compared to V_t. The above equation can be modeled in discrete time steps with the following formula:

$$\Delta Z = -V_t \cdot \Delta t + (2 \cdot k \cdot u_* \cdot Z \cdot \Delta t)^{1/2}\Delta W \qquad \text{equation (4a)}$$
$$\Delta X = u_w(Z) \cdot \Delta t \qquad \text{equation (4b)}$$

Gaussian white noise (ΔW) can be modeled by drawing randomly from a normal distribution. Figure 2 illustrates how trajectories were simulated by this model.

We tested the model described above with various values of Δt, and found that the model was rather insensitive for Δt. The model produced irrealistic results only for larger values of Δt. We chose the value of 0.001 s to avoid this problem.

Four species were selected on the basis of seed weight and the presence of plumed seeds for testing the model (Table 1). Seed shadows of these species were measured in a horizontal wind tunnel at two wind speeds (2 and 3 $\mathrm{ms^{-1}}$). At a wind speed of 6.5 $\mathrm{ms^{-1}}$ only seeds without plumes were released because the dispersal of plumed seeds at this wind speeds exceeds the length of the measuring compartment. The wind tunnel was a closed circuit and had a measuring compartment of 13 m long and a cross-section of 75 cm x 75 cm. Van Dorp et al. (1996) and Strykstra et al. (1998) used the same wind tunnel for their experiments. Seeds were released at a height of 40 cm. With a flexible tube seeds were brought from outside the wind tunnel to the release point in a perpendicular direction to the wind flow. The surface of the tunnel was covered with sticky wallpaper to trap the seeds at the point they reached the ground. The dispersal distance along the length of the wind tunnel was measured for each seed with an accuracy of 1 cm.

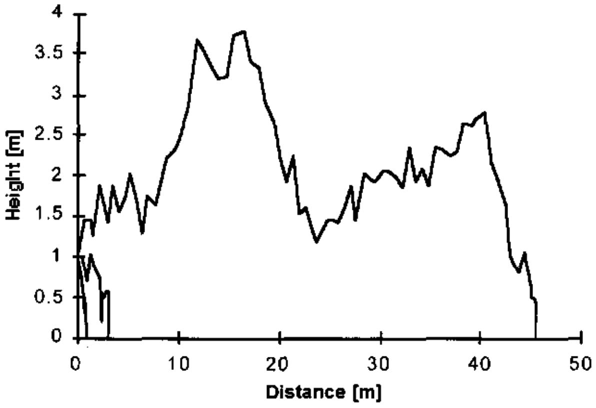

Figure 2. Three illustrative flight trajectories, selected from model simulations (terminal velocity 1 ms^{-1}; flowering and vegetation height respectively 1 and 0.5 m; wind speed 20 ms^{-1} at a reference height of 10 m). Co-ordinates for the figure are taken each 50 time steps.

The model was used to produce seed shadows of the selected species under the conditions of the horizontal wind tunnel. For one seed shadow 1000 runs were done. All 20 measured V_t-values resulting from the dropping method (or floating method for *Crepis*) were used 50 times. Wind profile parameters were fitted to a measured wind profile in the wind tunnel (for 2, 3 and 6.5 ms^{-1} respectively z_0 was $9.80*10^{-5}$, $1.15*10^{-4}$, $2.30*10^{-8}$ and u_* 0.1, 0.175, 0.17; *d* was 0 in all cases). The simulated trajectories started 40 cm above ground and were not allowed to exceed the height of the wind tunnel (75 cm).

Model sensitivity

The model was used to derive seed shadow predictions for the four species under grassland conditions. For two species, with approximately equally heavy seeds, *Picris hieracioides* L. and *Silene latifolia ssp. alba* (Mill.) Greuter & Burdet, three different aspects of the model were studied: wind speed, vegetation height and terminal velocity input. Starting with basic conditions: flowering height of 80 cm for both species, vegetation height of 60 cm, wind speed of 12 ms^{-1} and all 20 V_t-values of the dropping method. First the wind speed (u_w) was varied (6, 12 and 24 ms^{-1}, corresponding with forces of 4, 6 and 9 on the Beaufort scale), secondly vegetation height (z_v) (20, 40, 60, 80 and 100 cm) and finally terminal velocity per species (all data, mean, minimum and maximum of the results of the dropping method). The flowering height was estimated using known height ranges (Van der Meijden 1996). Goudriaan (1977) gives formulas to estimate z_0 and d with vegetation height (z_v):

$$\log d = 0.9793\ (\log z_v) - 0.1536 \qquad \text{equation (5)}$$

$$\log z_0 = 0.997\ (\log z_v) - 0.883 \qquad \text{equation (6)}$$

The friction velocity was calculated from equation (2a), when z_0 and d were estimated and u_w chosen at a reference height of 10 m, which is a reference height used in meteorology stations.

Results

Terminal velocities

The averages and ranges of V_t-values measured with the fall tower and the vertical wind tunnel are listed in Table 1. The mean weight (n=20) of the used seeds are also shown. In Figure 3 the V_t-values of the floating method are plotted against those of the dropping method per species. In general results of both methods were in the same order, especially when the large ranges in V_t-values are considered (Table 1). Only for high (> 3 ms^{-1}) values of V_t the results of the floating method were all found to be lower than the results of the dropping method.

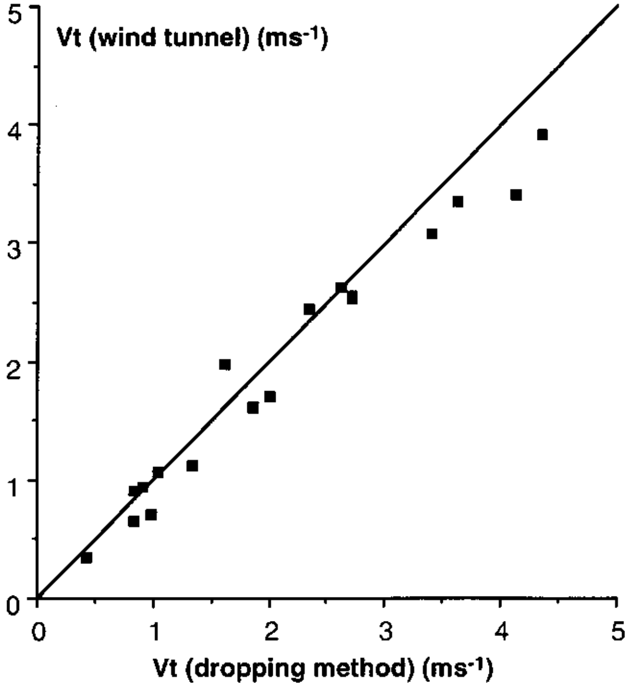

Figure 3. The mean average terminal velocity-values [m s^{-1}] resulting from the floating method plotted against terminal velocity-values from the dropping method. A 1:1 line facilitates comparing the methods.

Model and test

Cumulative seed shadow curves were constructed with the measured and simulated dispersal distances (Figures 4 and 5). Figure 4 depicts these curves for *Crepis* and *Picris* (both species with plumed seeds) based on the results from the model. For *Picris* the median, slope and tail of the measured curves were approached closely by the simulated curves. For *Crepis* the measured medians met well at 2.0 ms^{-1}, however at 3.0 ms^{-1} less well. The slopes fit well in both cases. But the tail of the measured curves at 2.0 ms^{-1} was lower than simulated.

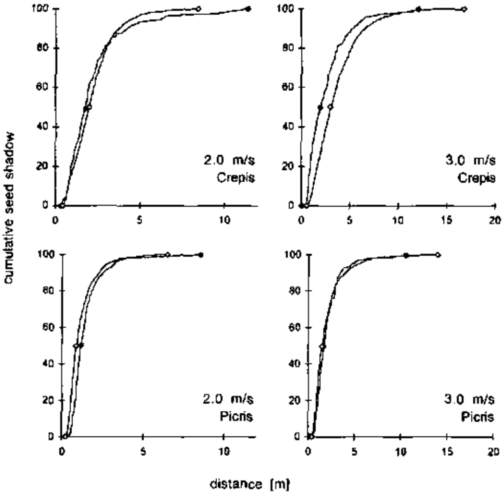

Figure 4. Cumulative seed shadows of: 1) horizontal wind tunnel experiment, closed circles, 2) simulation results, open diamonds. The seed shadow diagrams differ in wind profile (2 and 3 ms^{-1}) and species (*Crepis capillaris* and *Picris hieracioides*).

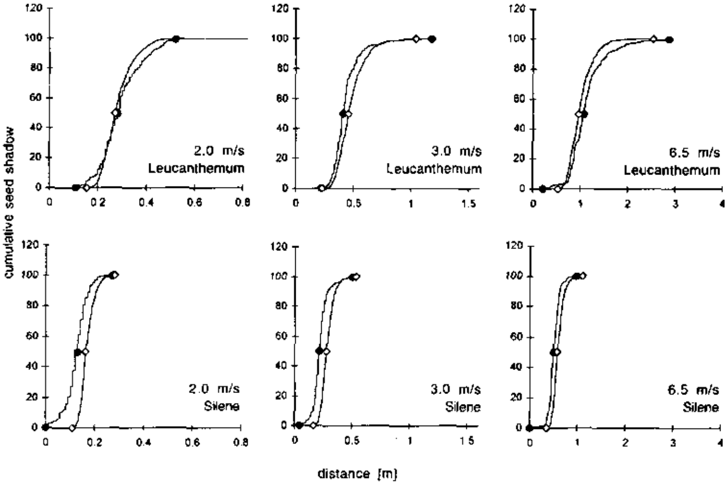

Figure 5. Cumulative seed shadows of: 1) horizontal wind tunnel experiment, closed circles, 2) simulation results, open diamonds. The seed shadow diagrams differ in wind profile (2, 3 and 6.5 ms^{-1}) and species (*Leucanthemum vulgare* and *Silene latifolia ssp. alba*).

For *Leucanthemum vulgare* Lamk. the median distances of the simulations fitted very well, for *Silene* there was a slight, persistent overestimation of median distances (Figure 5). The slope of the simulated curves resembled that of the measured ones rather well for *Silene*, though for *Leucanthemum* they were a bit steeper at 2.0 ms^{-1}. The tails of the *Silene* simulation curves fit the experimental results better than the simulation curves of *Leucanthemum*, where especially at 2.0 and 6.5 ms^{-1} the measured curve tail lay lower. This means that relatively more seeds are dispersed a relative great distance.

Model sensitivity

The model simulations with varied field parameters resulted in cumulative seed shadows. These diagrams have logarithmic scales on the distance-axes and are therefore not directly comparable with the model-test diagrams. At double wind speed the median dispersal distance also doubled for *Picris* and *Silene* (Figure 6). Tail distances (95 and 99 percentiles in Table 2) on the other hand were more affected by wind speed. For both species the tail distances increased about 3.3 times at a doubled wind speed.

Taller vegetation led to smaller median dispersal distances in all cases (Figure 7). As long as the release height is above the vegetation, a decrease in vegetation height of 20 cm doubles median dispersal distances. In the case of a vegetation height of 100 cm (20 cm higher than the release height), about 20% of the simulated *Picris* seeds and 60% of the *Silene* seeds did not come further than 1 mm. In contrast to the trend in median dispersal distances, the tail distances (95 and 99 percentiles in Table 3) show increasingly less differences at different vegetation heights.

The effect of using different V_t-values is plotted in Figure 8. For both species the median dispersal distances generated with the total range of V_t-values are best approached by the medians generated with the mean V_t-value (Table 4). When only the minimum V_t-value was used the median was higher, and when only the maximum V_t-value was used the median was lower. The tail dispersal distances of the four curves are all different for *Picris*, with increasing distances in the order: maximum, mean, range and minimum of the V_t-values. Silene shows the same pattern, but here the mean-curve approaches the all data-curve in the tail very well too.

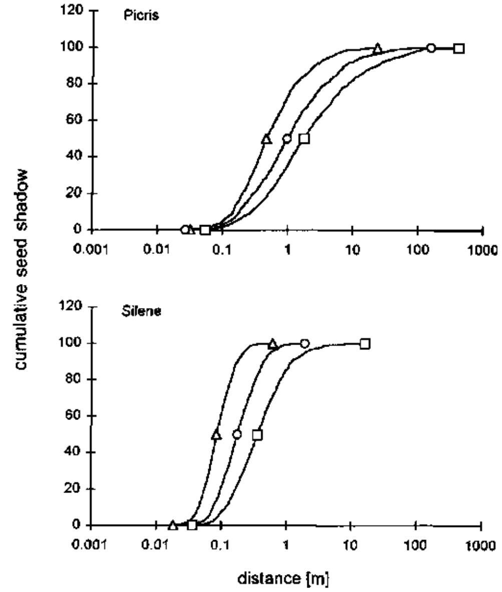

Figure 6. Cumulative seed shadows for *Picris hieracioides* and *Silene latifolia subsp. alba* resulting from model simulations. Wind speeds are varied from 6 (triangles) to 12 (circles) and 24 (squares) ms^{-1}, at a reference height of 10 m. Flowering and vegetation heights are 80 and 60 cm respectively.

Table 2. The 50 , 95 and 99 percentile distances [m] of *Picris hieracioides* and *Silene latifolia* ssp. *alba* per wind speed (6, 12 and 24 ms^{-1} at a reference height of 10 m, see also Figure 6) flowering height was 80 cm and the vegetation height 60 cm.

Species	Percentile	Wind speed (ms^{-1})		
		6	12	24
Picris	50	0.47	0.96	1.76
	95	4.37	14.31	51.60
	99	11.91	46.01	118.46
Silene	50	0.09	0.18	0.36
	95	0.22	0.57	1.98
	99	0.31	0.91	3.96

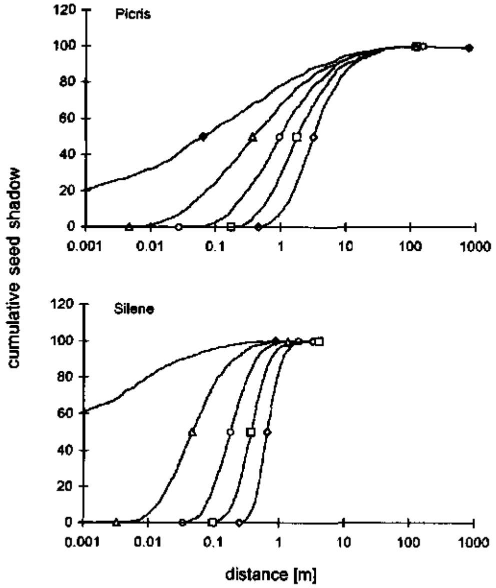

Figure 7. Cumulative seed shadows for *Picris hieracioides* and *Silene latifolia subsp. alba* resulting from model simulations. Vegetation heights are varied from 20 (open diamonds) to 40 (open squares), 60 (open circles), 80 (open triangles) and 100 (closed diamonds) cm. Flowering height is 80 cm and wind speed 12 ms^{-1} at a reference heights of 10 m.

Table 3. The 50 , 95 and 99 percentile distances [m] of *Picris hieracioides* and *Silene latifolia* ssp. *alba* per vegetation height (20, 40, 60, 80 and 100 cm, see also Figure 7) flowering height was 80 cm and the wind speed 12 ms^{-1} at a reference height of 10 m.

Species	Percentile	Vegetation height (cm)				
		20	40	60	80	100
Picris	50	3.21	1.77	0.96	0.38	0.06
	95	23.79	20.82	14.31	14.82	10.88
	99	42.50	47.96	46.01	52.93	51.07
Silene	50	0.65	0.37	0.18	0.05	0.00
	95	1.37	0.91	0.57	0.31	0.09
	99	1.81	1.66	0.91	0.68	0.29

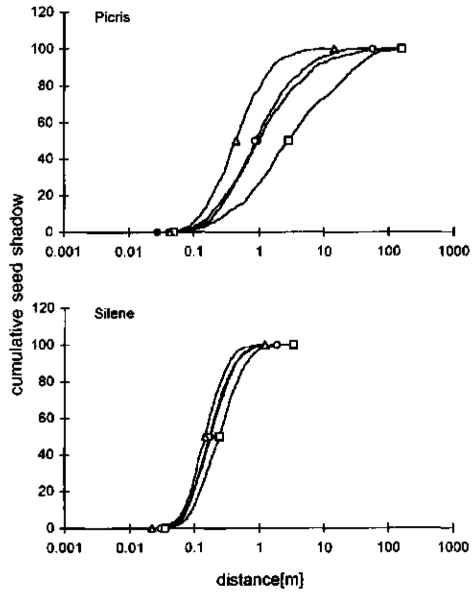

Figure 8. Cumulative seed shadows for *Picris hieracioides* and *Silene latifolia* ssp. *alba* resulting from model simulations. V_t-inputs are varied (maximum, open triangles; mean, open circles; all data, closed circles; minimum, open squares). Flowering and vegetation heights are 80 and 60 cm, respectively. The wind speed is 12 ms^{-1} at a reference heights of 10 m.

Table 4. The 50 , 95 and 99 percentile distances [m] of *Picris hieracioides* and *Silene latifolia* ssp. *alba* per terminal velocity V_t- input ('all data' denotes all 20 V_t values are used 50 times in the simulations, 'Mean', 'max' and 'min' denote respectively that the mean, maximum and minimum values of the 20 V_t values is used 1000 times, see also Figure 8) flowering height was 80 cm while the vegetation height was 60 cm and the wind speed 12 m s^{-1} at a reference height of 10 m.

Species	Percentile	V_t input			
		all data	mean	max	min
Picris	50	0.96	0.86	0.44	2.81
	95	14.31	9.09	2.37	47.85
	99	46.01	18.23	5.26	115.52
Silene	50	0.18	0.17	0.15	0.24
	95	0.57	0.58	0.42	0.83
	99	0.91	0.85	0.73	1.44

Discussion

Comparison of methods to determine V_t

For five of our species comparison with V_t-values in literature is possible (Table 5). In general our results were in the same order as V_t-values found by others. However no conclusions can be made because different authors used different seed samples.

The comparison between V_t-values from the different methods (Table 1) indicates that the methods differ only at high V_t-values. An underestimation of high V_t-values from the vertical wind tunnel might be possible, since it is difficult to create a totally laminar air flow of high speed. Aberrant wind speeds from the measured average may lift the seeds when a laminar air low of the same average wind speed is not able to do so (Hofstee 1992). However, all differences should be viewed in light of the great ranges within the data set (see Table 1, Andersen 1992, Geritz 1995) and the fact that different seed samples (from the same population) are used. In general can be concluded that the two methods produced comparable results in the range of species measured.

Comparison of V_t-values between species

Fenner (1985) stated that heavier seeds are dispersed less far. Results show that morphologic wind-dispersal adaptation has more influence on V_t-values than seed weight for the four species. A crude sequence from low to

Table 5. Terminal velocity (ms^{-1}) of five species. Comparison between literature and measured values.

Species	Dropping method	Floating method	Literature
Daucus carota	2.01	1.71	1.16(9)
Hieracium pilosella	0.98	0.71	0.49(4)
Hypochaeris radicata	-	0.54	0.32(6), 0.41(8), 0.43(2), 0.67(3)
Picris hieracioides	0.83	0.65	0.13(9), 0.47(5)
Rumex obtusifolius	2.72	2.53	1,26(3)
Taraxacum officinale	0.43	0.34	0.31(1), 0.33(7), 0.36(8), 0.42(5), 0.45(3), 0.66(2)

(1) Andersen 1992, (2) Andersen 1993, (3)Askew et al. 1997, (4) Hensen & Müller 1997, (5) Matlack 1987, (6) Ridley 1930, (7) Schulz et al. 1991, (8) Sheldon & Burrows 1973, (9) Verkaar et al. 1983.

high V_t-values can be seen when all 21 species are taken into account: plumed and winged seeds followed by grass seeds with lemma's and finally other not wind adapted seeds. Although 3 species with seeds heavier than 2 mg, all have high (>2.5 ms^{-1}) V_t-values, an overall relation between mere seed weight and V_t-value is not present. This may lead to the conclusion, that terminal velocity and thus wind dispersal, within the range of herbaceous plants (with seeds of 0.1 to 2.0 mg), is more determined by seed morphology than by seed mass.

Generality of Andersen's model

The median and tail of the seed shadows were of the same order and the slopes of the curves of the simulated distances also seem realistic. This confirms that this kind of individual-based model with stochastic turbulence can be used to give reliable estimations of seed shadows of herbaceous species. On the other hand wind tunnels are only a limited representation of field circumstances, where other processes may occur. However, Andersen (1991) showed a good performance of the model for one plumed species under field conditions. Considering the diversity in the seeds used in the mentioned experiments the overall impression is that the model simulations make sense and that this kind of model is a useful tool to estimate seed shadows.

Effect of wind speed, vegetation height and intraspecific terminal velocity range

The results of the sensitivity analysis show that the increase in median distance is proportional to the increase in wind speed. This is in agreement with the simple estimation of the dispersal distance: $X = u_w \times Z / V_t$ (Matlack 1987, Ernst et al. 1992, Greene & Johnson 1992), and field experiments done by Augspurger & Franson (1987) with artificial fruits. However the tail behaved differently. An increase of the wind speed by a factor 4, causes an increase in the tail distances (95 and 99 percentiles) by a factor 11. An explanation for this phenomenon can be found in the fact that the friction velocity grows linearly with wind speed (equation 2a), implicating stronger turbulence (equation (4a)) and greater variance in dispersal distances. Van Dorp et al. (1996) also found an exponential relation between wind speed and 99 percentile distances. The highest wind speed of 24 ms^{-1} (7.8 ms^{-1} at flowering height) is still an underestimation of wind speeds that can occur annually (Van Dorp et al. 1996).

The increase of vegetation height resulted in smaller median dispersal distances for both *Picris* and *Silene.* The tails of the seed shadows, however, are less affected by the height of vegetation. The 99 percentile of *Picris* even showed a small increase with vegetation height. Less median dispersal can be accounted for by the fact that the chance that a seed is 'captured' by vegetation almost directly increases for higher vegetation. On the other hand higher vegetation increases friction velocity slightly. This means that 'escaping' seeds above a high vegetation experience more turbulence, which can result in an increasing 99 percentile of the seed shadow. All this leads to the hypothesis that seed shadow tails are rather insensitive for vegetation height changes.

The results of the V_t-range analysis show that using the mean value of V_t instead of all V_t-data gives a good estimation of median distances, but underestimates the tail when slowly falling seeds are studied. This indicates that the spread in seed shadow is not only determined by turbulence, but also by variation in terminal velocities of seeds. Intraspecific variation in seed characteristics, and thus dispersal potentials, can therefore be subjected to evolutionary selection (Andersen 1993, Geritz 1995). However it should be noted that seed characteristics leading to good dispersal, may be disadvantageous for other survival strategies such as long dormancy (Venable & Brown 1988).

Conclusions

Two methods were compared to obtain terminal velocity values. Both methods have their practical advantages and disadvantages. However, we found both methods to produce comparable results within the range of measured terminal velocities.

Andersen's (1991) individual-based model was only tested for one species with plumed seeds. Now this model has been tested for four different herbaceous species which differ with respect to seed weight and presence of plumes. The model simulations showed remarkable resemblance with wind tunnel results given the different seed characteristics and wind speeds used. This indicates the generality of this model for herbaceous species. The model can easily be elaborated with a third dimension, wind speed fluctuations (in strength and direction), non-point sources, threshold release wind speed, probability density of seed release changes over wind speeds (Sharpe & Fields 1982, Greene & Johnson 1989, Andersen 1991) or other meteorological aspects like thermic updraft, which indicates a wide range of possible applications which may lead to more insight in wind dispersal of herbaceous seeds.

7

Effects of nutrients, disturbance, mowing and width on the dynamics and diversity of plant communities in field boundaries: an analysis using a spatially explicit competition model

Adapted from: P. Schippers & W. Joenje (submitted)

Abstract

To evaluate the effects of nitrogen, disturbance, mowing and boundary width on the composition of plant communities of field boundaries a spatial plant competition model was modified. The new simulation model incorporates competition for nitrogen and light as well as mineralization and population dynamical processes.

The model was parameterized for four grassland species: *Poa annua, Holcus lanatus, Anthoxanthum odoratum* and *Festuca ovina.* To test the model, simulation results were compared with data from a pot and a field experiment. In addition, several long-term simulations were performed to analyse the effect of the various factors on the field boundary composition.

The results of the simulations were generally in agreement with experimental results. The simulation study indicates that perennial diversity was maximal when nutrient input and degree of disturbance were low, the cuttings were removed and the boundary width was wide. It was concluded that the perennial diversity of the field boundary vegetation is promoted by the following measures:
1) preventing nutrient input from the arable field, 2) keeping the disturbance level under 20% of the area, 3) mowing and removing of the cuttings, and 4) keeping the boundary at least wider than maximum fertilizer misplacement.

Key words: Succession, diversity, field boundary, field margin, nitrogen, nutrients, extinction, plant competition, old field succession, modelling, *Anthoxanthum odoratum, Festuca ovina, Holcus lanatus, Poa annua*

Introduction

Over the last decades, the natural plant diversity has been reduced in many agricultural landscapes (Boatman 1992, Joenje & Kleijn 1994, Freemark & Boutin 1995). The field boundary, the strip of semi-natural vegetation bordering most arable fields is an important area for plant species survival and diversity in landscapes dominated by agriculture. Decreases in plant species diversity were generally linked with the intensification of agricultural land use, causing a reduction of area, an increment of disturbance is and input of agro-chemicals in arable field boundaries (Joenje 1991, Snoo 1995, Kleijn 1997).

Considering the drift of agro-chemicals into the field boundary especially the load of nutrients can be regarded as an important determinant of the plant species diversity (Kleijn & Snoeijing 1997). Larger nutrient availability generally leads to an increase of competitive asymmetry among plant species which generally leads to a quick exclusion of short, slowly growing plant species (Keddy et al. 1997, Chapter 3).

Disturbance can be regarded as an important source of uncertainty for plant species in herbaceous vegetation (Holzapfel et al. 1993, Firbank 1993). Grime (1979) considered disturbance as one of the two most important factors that define primary strategies and shape the composition of plant communities.

Disturbance in field boundaries can be caused, for instance, as a side effect of farming operations or by spot application of broad spectrum herbicides (Snoo 1995). Disturbance has two effects it causes species loss by mortality, and it opens up space for colonizers from elsewhere, which might increase species diversity (Begon et al. 1990).

Another human impact on field boundary vegetation related to disturbance is mowing. This is mostly done to prevent woody species to establish in boundaries and is generally considered to enhance diversity (Bakker 1989, Bakker & Olff 1995). Mowing in field boundaries is often done after harvesting because then the boundary is accessible for mowing equipment. Cuttings may be removed or left behind, each with its consequences for the nutrient cycle.

The width of the field boundary may be considered an important determinant of diversity since the number of species in a vegetation is strongly related to area (Joenje 1999). Increase of the boundary width will extent the area of semi-natural vegetation which leads to increased diversity in agricultural landscapes.

Additionally wide boundaries may provide shelter from agro-chemicals that are often inaccurately distributed (Melman & Van der Linden 1988, Rew et al. 1992, Snoo 1995) This also may cause a that wide boundaries have a higher biodiversity.

To obtain a good impression of the effect of various factors on plant diversity and vegetation dynamics in field boundary communities experimentally, a large and long-term experiment would be needed. A suitable simulation model, however, may give a quick insight in to the effects of various treatments on field boundary vegetation. In Chapter 4, the model VEGPOP1 was developed that was able to handle complex spatial competition among grassland species. This model, when extended with modules that describe processes of disturbance, dispersal, population dynamics and decomposition of dead material may yield a potentially interesting tool to describe complex vegetation dynamics of field boundaries over a longer time span. In this paper we add these modules to the VEGPOP1 model and we compare simulations of this new model (VEGPOP2) with a competition experiment on an old arable field and a pot experiment described in Chapter 3. We use VEGPOP2 to answer the following question: What are the effects of: fertilizer load, disturbance by farming operations, boundary width and mowing on the species composition and on diversity of the field boundary vegetation?

Field experiment

From 1 May 1994 until 15 September 1996 a competition experiment was carried out on an old arable field on sandy soil in Wageningen, The Netherlands. Eight species were selected to represent a successional sequence from an arable weedy stage to a perennial vegetation of nutrient-poor habitats (Table 1). These eight species were sown in plots of 2.5 × 2.5 m^2 at a density of 50 seeds per m^2 for each species. Two nutrient levels were established, by applying 133g NPK fertilizer per m^2 (15% nitrogen, 12% phosphorus and 24% potassium, N20 treatment) whereas no nutrients were applied in the N0 treatment. The nutrient were applied at 1 June of each growing season. On 15 September of each year a square meter of the plots was harvested, while the rest of the plot was mown. At each harvest, the above-ground dry weight of each species was measured as well as the plant height. During the last season of the experiment nitrogen mineralization of the soil was measured using the *in situ* method described by Raison et al. (1987).

Table 1. Selected species in relation to their successional position and plant groups.

Habitat	Species Groups	
	Grasses	Herbs
1) Nutrient rich (weedy)	*Poa annua*	*Chenopodium album*
2) Nutrient rich (peren)	*Holcus lanatus*	*Rumex obtusifolius*
3) Intermediate rich	*Anthoxanthum odoratum*	*Plantago lanceolata*
4) Nutrient poor	*Festuca ovina* Ssp. *tenuifolia*	*Hieracium pilosella*

Model description

General model description

VEGPOP2 is a modified version of the VEGPOP1 model (Chapter 4). In both versions space is represented by a lattice. In each cell of this lattice the vegetation is considered to be a mixture of species competing for light and nitrogen (N is considered to be the limiting nutrient) (Figure 1). The models keep track of the biomass and number of plants per species per cell. For a detailed description of the simulated processes of VEGPOP1 we refer to Chapter 4. In this chapter we will describe the differences between both versions.

In VEGPOP2 population dynamical processes were added, based on the spatial population dynamical model of Chapter 5. In addition, wind dispersal processes were incorporated according to the model of Chapter 6. To simulate the decomposition of dead material and mineralization a routine adapted from Bloemhof & Berendse (1995) was added (Figure 1). Finally, some insensitive processes in VEGPOP1 (see Chapter 4) were simplified and the biomass allocation to the inflorescence was modified to allow for annual allocation patterns.

Model simplifications

Insensitive processes of VEGPOP1 were simplified in the following way (according to Chapter 4) First, the maintenance respiration and photosynthesis were integrated to one simple light efficiency value (E in g DM/MJ) according to Schapendonk et al. (1998). Second, the module that simulate storage of reserves were removed and third, the nitrogen routine

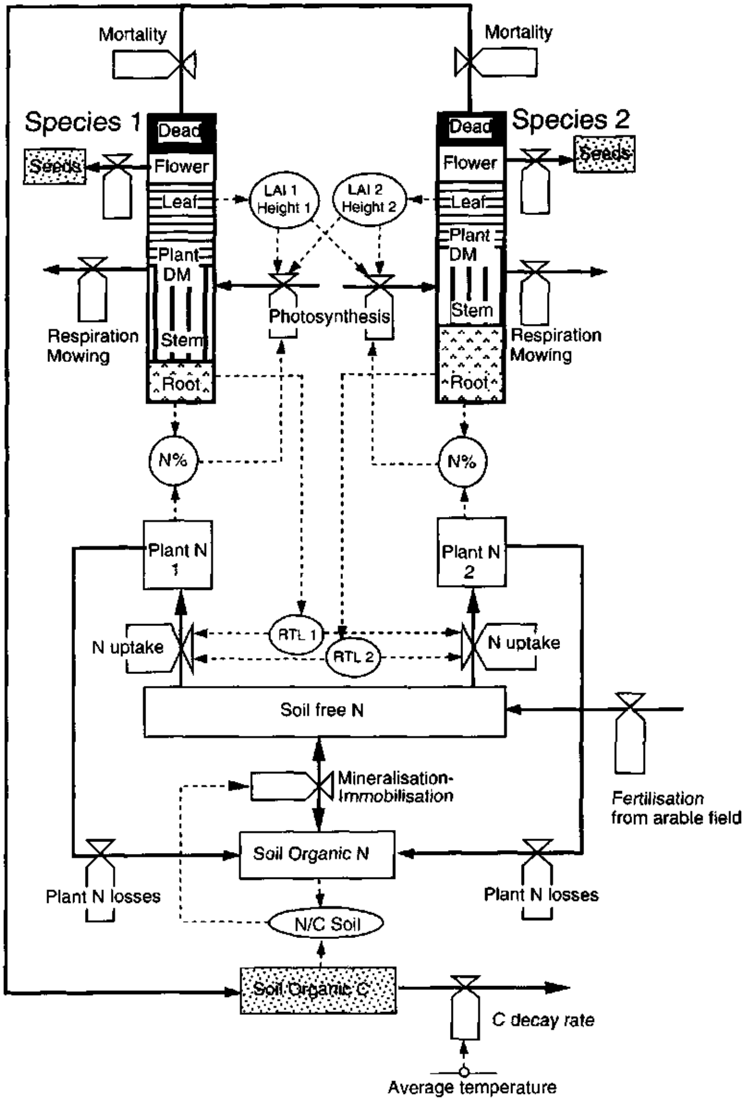

Figure 1. Simplified flow diagram describing the competition between two species for light and nitrogen and the decomposition as modelled in the VEGPOP2 model. White squares represent nitrogen states whereas dotted and shaded area represents dry matter states. Dashed lines is information flow and solid line represents flow of matter.

was simplified so that all shoot cohorts were assumed to have the same nitrogen concentration, as in the model of Seligman & Van Keulen (1981).

Modification in allocation to reproductive organs

In VEGPOP2, the allocation routine is slightly modified. In VEGPOP1 the allocation to the flowers was defined as a fraction of the total production during flowering. The remaining assimilates were divided between shoot and root. A constant fraction of the shoot was considered to be leaves. This might be a satisfactory solution for perennial species with a rather constant leaf-stem fraction, but in annual species such as *Poa* this is not the case, since flowers grow mainly at the expense of the leaves (Chapter 2). In the VEGPOP2 model we made allowances for this.

Dispersal

At the end of the flowering period the biomass accumulated in the flowers is converted into seeds by dividing the biomass of the flowers by the seed weight. Dispersal from the source cell is defined by a dispersal vector which contains cumulative dispersal probabilities. A dispersal vector can be assigned to a certain species. Arrival probabilities for a species were calculated with a simulation model SEEDTRIP (Chapter 6). Two hundred thousand individual seed trajectories were calculated using 20 terminal velocities. For these calculations, summer wind speed probabilities of a meteorological station in Eelde (The Netherlands) were used (Oemraw 1985). Arrival distances of each trajectory were used to obtain the cumulative probability density curves for each species (Table 2). In the VEGPOP2 model, spatial seed shadows from this probability density curve were obtained by drawing a dispersal distance from this distribution for each seed. The direction of dispersal was chosen at random. When seeds were dispersed outside the field boundary seeds were lost and when seeds were dispersed along the direction of the boundary toroidal rules were used.

Disturbance

In this chapter we use the disturbance definition of Begon et al. (1990): 'any relatively discrete event in time that removes organisms and opens up space which can be colonized by individuals of the same or different species'. The disturbance, which varies between 0 and 100 % of the area, is timed in spring when soil cultivation activities are intense (Table 3). If a cell is disturbed, plants in the cell die and new plants are recruited from the seed bank. This is

Table 2. Distance (m) of different cumulative probabilities, calculated using the model SEEDTRIP of Chapter 6 and summer wind speed probabilities of Eelde (The Netherlands).

	Poa	*Holcus*	*Anthoxanthum.*	*Festuca*
Terminal velocities (m/s) (Chapter 6)				
min.	1.81	0.63	1.02	0.80
mean	2.34	0.84	1.86	1.62
max.	2.95	2.02	2.99	2.66
Height (m) (from Grime et al. 1988)				
flowers	0.30	0.60	0.50	0.45
vegetation	0.15	0.35	0.15	0.15
Distance (m) at cumulative probability				
0.010	0.005	0.02	0.02	0.02
0.050	0.02	0.08	0.06	0.06
0.100	0.03	0.11	0.09	0.08
0.250	0.04	0.19	0.14	0.13
0.500	0.07	0.36	0.24	0.23
0.750	0.12	0.80	0.42	0.41
0.900	0.21	1.75	0.73	0.75
0.950	0.29	2.68	1.04	1.12
0.990	0.59	8.31	2.18	2.55
0.999	1.47	38.13	5.63	7.71
0.999995*)	7.13	360.49	78.34	72.66

*) *highest distance out of 200000 trajectories*

achieved by germination following disturbance. The level of disturbance is defined as the proportion of cells affected, and is distributed at random.

Because disturbance is often caused by mowing (visible observation in the experiment) we introduced a second disturbance event of 20% following mowing in autumn. This disturbance event gave rise to a second germination opportunity like in the model described in Chapter 5.

Population dynamics

In the model a x,y lattice represented the space. Every cell of the lattice could contain several species in competition. Adult plants were able to move into adjacent cells if their area exceeded the cell area (vegetative expansion). A fraction of the assimilates was invested in seeds during the flowering period.

This period was determined by the temperature sum since 1 January as measured in the field experiment. At the end of the flowering period, the accumulated biomass in flowers was turned into seeds that were dispersed according to a probability density curve over the lattice. Arrived seeds germinated or died. As in the model described in Chapter 5, seeds only germinated in cells which were not dominated by adult plants. When the total leaf area index (m^2 leaf/m^2 area) of all adult species in a cell was less than 0.5 germination was allowed.

Seeds germinated mainly in disturbed cells. In a cell seedlings competed with adults and other seedlings for nitrogen and light. During seedling competition self thinning of seedlings occurred according to the self thinning rule of Yoda et al. (1963). At a certain day of the year seedlings turned into adults and the biomass was merged (fusion) with the corresponding adult of the cell. For an overview of events see Table 3.

Table 3. Sequence of events in the model VEGPOP2.

Date	Event
15 March	Fusion between seedling (17 Sept.) and adult
31 March	Disturbance (variable 0-100%)
1 April	Germination in disturbed cells
1 May	Start of the simulation (first year)
1 June	Fertilization (0-10 gN m^{-2})
1 August	Fusion between seedling (1 April) and adult
1 October	Mowing at 5 cm height
2 October	Disturbance caused by the mowing treatment (20%)
3 October	Germination in disturbed cells
31 December	Seed mortality of seeds in the soil

Decomposition of plant material

The decomposition routine is based on the algorithm described by Bloemhof & Berendse (1995). When plants or plant parts die the dry matter is added to the soil. The model distinguishes between 'green' material and dead material. The 'green' material originates from thinned seedlings, disturbed plants and not removed cuttings whereas the dead material originates from natural turnover induced by the plant. The green material has the same N concentration as the plants because plants have no time or need to withdraw their nitrogen during processes like thinning, disturbance and mowing. This plant material enters soil-pool 1, where soluble N and C leaches relatively quickly to the dissolved N pool. The average residence time in this pool is 30 days after which the content flows into soil-pool 2. Pool 2 also receives 'dead' material directly from plants. The average residence time in this pool is two , and the N/C ratio determines the mineralization or immobilization (Bloemhof & Berendse 1995). From pool 2 matter flows to the the long-term soil-pool 3 where a slow but steady decomposition occurs.

Because leaves have other decomposition properties than stems and roots (Bloemhof & Berendse 1995) pool 1 and 2 have each two separate compartments. One is for leaf material and the other is for stem and root material which are decomposed at a slower rate.

Mineralized N from various pools goes to the free-N pool. Free N might be taken up by the plant or might be lost from the rooted zone by leaching. The leaching of free N is calculated from a simple water balance based on the Penman equation (Kropff & Van Laar 1993), under the assumption that every grid is covered by vegetation.

Parameters of this system were taken from decomposition data of Bloemhof & Berendse (1995) who measured their decomposition parameters on the same field that we used. Further, the C and N content of the experimental soil was measured (1.5% C and 0.1% N) as well as the organic matter content (2.4%). The decomposition rate of pool 3 was calibrated using the mineralization data obtained in the experiment. This calibration was done under the assumption that pool 2 contain 461 g m^{-2} organic matter (= yearly productivity of the vegetation) while the rest of the organic matter was present in pool 3.

Species parameterization

The plant parameters for *Holcus*, *Anthoxanthum* and *Festuca* were the same as used in Chapter 4 with the exception of the shoot turnover of *Anthoxanthum*, since this value appeared to be rather low (Table 4). In Chapter 2 we found a much longer leaf longevity value for *Anthoxanthum* (1405 °Cd). Since the latter value was more in line with the expectation that species adapted to moderate nutrient-rich environment have intermediate biomass turnover, the latter value is used for *Anthoxanthum*. The values of *Poa annua* were mainly based upon the experiment of Chapter 2 with the exception of the root turnover which was assumed to be the same as that of

Holcus.

Parameters for dormancy and germination were based on Thomson et al. (1997). Although the reviewed data are quite variable, this study indicates that *Poa* and *Holcus* have a stable seed bank whereas *Festuca* and *Anthoxanthum* have short living seeds. Because of the variability of the data we follow the parameterization of Chapter 5. For the species with long-lived seeds (*Holcus* and *Poa*) the values for annual seed mortality as well as the germination probability were set at 0.1, implying that seeds have an average longevity of 5 years which is considered a persistent strategy (Bakker et al. 1996). For the plants with non dormant seeds (*Festuca* and *Anthoxanthum*) the germination probability was set at 0.9 while the rest died. This is considered transient seed bank (Bakker et al. 1996).

Simulations

Testing the effect of model simplification

To evaluate the effect of simplification we simulate the pot experiment of Chapter 3 with the modified model for the most complex case: a mixture of *Festuca, Holcus* and *Anthoxanthum.* The simulations were done in nutrient-rich conditions (receiving of 20 g N m^{-2} yr^{-1}) and at a low nutrient level (no nutrient gift). The simulations were compared with data from the experiment and with simulation results of the model VEGPOP1 (Chapter 4).

Reference simulation conditions

All other simulations were performed with a mixture of *Poa annua, Holcus lanatus, Anthoxanthum odoratum* and *Festuca ovina* as parameterized in Table 4. Simulations started with 50 seedlings per m^2 of each species, and the biomass of the seedlings equalled the weight of the seed. The soil was parameterized to represent the soil of the experiment. The cell size of all simulations was 16.66×16.66 cm^2 the same as the pot size in the experiment of Chapter 3. The maximum adult plant density was 100 plants m^{-2} per species which is the same adult density as used in Chapter 5.

Simulating the field experiment

To compare the performance of the model with the field experiment we ran the model in the weather and soil conditions of the field experiment. This was done by simulating one m^2 vegetation. The edges of the simulated area

Table 4. Parameters used in the VEGPOP2 model for the species *Poa annua*, *Holcus lanatus*, *Anthoxanthum odoratum* and *Festuca ovina*.

Assign.	Description(unit)	Poa	Holcus	Anthox.	Festuca	Source
Physiological parameters						
E	Light use efficiency (g DM/MJ PAR)	2.71	2.71	2.71	2.71	(L) Schapendonk et al. (1998)
k	Extinction coefficient	0.6	0.6	0.6	0.6	(L) Schapendonk et al. (1998)
Allocational parameters						
F_l	Fraction leaves(g leaves/g shoot)	0.59	0.48	0.52	0.68	(M) Chapter 4
F_m	Minimum shoot fraction	0.58	0.32	0.38	0.44	(M) Chapter 4
F_x	Maximum shoot fraction	0.87	0.72	0.82	0.87	(M) Chapter 4
Parameters determining turnover						
T_{sh}	Temp. sum determining shoot longevity(°Cd)	1089	1265	650	1965	(M) Chapter 3
T_f	Temp. of freezing det. shoot longevity (°Cd)	10	97	163	655	(M) Chapter 3
F_r	Root mortality factor (1/d)	0.00371	0.00371	0.00341	0.00282	(O) Chapter 3
Parameters determining Nitrogen economy						
N_m	Maximum N conc. (gN/gDM)	0.02	0.02	0.02	0.02	(P) Spitters (1989)
N_c	Critical N concentration (gN/gDM)	0.0135	0.0135	0.0135	0.0135	(P) Spitters (1989).
N_r	N concentration of the Roots (gN/gDM)	0.006	0.006	0.006	0.006	(P) Spitters (1989)
N_m	Minimum N conc. of the plant (gN/gDM)	0.005	0.005	0.005	0.005	(P) Spitters (1989).
Architectural parameters						
SRL	Specific root length (m/g root)	294	316	306	380	(M) Chapter 2
SLA	(N0) Specific leaf area dm_2/g leaf)	4.0*	variable	true the season		(M) Chapter 3
SLA	(N20) Specific leaf area dm_2/g leaf)	2.7*	variable	true the season		(M) Chapter 3
R	Height Width Ratio	1.9	3.4	2.2	2.1	(U) Chapter 2
V	Volume per gram shoot (l/g DM shoot)	0.82	1.13	0.53	0.61	(U) Chapter 2
Flowering						
$STAFL$	Temperature sum where the flowering starts	721	724	512	512	(M) Field experiment
$FINFL$	Temperature sum were the flowering ends	2500	1694	1252	1252	(M) Field experiment
$MFRFL$	Maximum allocated to flowers	0.51*	0.14	0.14	0.14	(M) Harper (1977)
Population dynamics						
$SDGFR$	Germination fraction of the seeds	0.1	0.1	0.9	0.9	(P) Chapter 5
$SDMFR$	Mortality fraction of the seeds	0.1	0.1	1.0	1.0	(P) Chapter 5

P = general plant value, L = *Lolium perenne* value used, M = measured on the same species, O = obtained by optimizing, U = unpublished but measured in the experimental situation. * *Poa* values from chapter 2.

in the model were treated as a torus in all directions for both seeds and plants. To avoid the complexity of the interaction between eight species we used the four grasses to represent the different successional stages in the experiment. The biomass just before mowing was taken as the value for evaluation.

Scenario analysis nitrogen and disturbance

To obtain insight in the effect of disturbance and nutrient load on the outcome of species competition in the arable field boundary, simulations were performed at various nitrogen loads (0, 1, 2, 5, 10 g N m^{-2}) and disturbance levels (0, 11, 25, 50, 75, 89, 100 % of cells). This was done by simulating one m^2 in standard conditions over ten years, using weather data of Wageningen meteorological station from 1985-1994. In the Y direction neighbouring cells outside the simulated area represent neighbouring boundary vegetation. In this direction the edge of the simulated area for both seeds and plants were modelled as a torus. In the X direction area outside the simulated area represent the arable field. Therefore this edge was made impermeable for plants and was permeable for seeds. Seeds that cross the border to the arable field were removed from the system. The simulation was started at 1 May 1985. As a measure for evaluation the mean value (three reruns) of the maximum shoot biomass in the final year was taken. All simulations were performed for three mowing treatments: 1) mowing at 5 cm height and removal of the cuttings, 2) mowing at 5 cm height and leaving the cutting in the field and 3) no mowing and no mowing-related disturbance.

Scenario analysis: boundary width

To investigate the impact of field boundary dimension on the vegetation dynamics, simulations were performed with a boundary width of 0.16, 0.5, 1.0 and 2.0 meters. In these simulations the disturbance in spring was zero whereas in the treatments where mowing occurred the mowing-related disturbance in autumn was still present. Further conditions were identical to those described in the last section.

Nitrogen load may not be distributed homogeneously over the boundary area but more likely as a gradient with large N values near the arable field (Melman & Van der Linden 1988, Rew et al. 1992). To analyse this effect we ran a series of simulations using a nitrogen gradient perpendicular to the field boundary which drops linearly to zero over 2 meter. When the boundary width was smaller than 2 meters this gradient was maintained which resulted in the same dose for cells at the same distance from the field edge.

Definition of diversity

In this study we define diversity as the state where all species have the lowest probability to become extinct. This implies that the state where all species coexist with a large biomass over a long period is considered the most diverse state. Therefore we use the Shannon index that takes presence and biomass into account (Shannon & Weaver 1949):

$$D = -\sum_{i=1}^{n} \left(F_i \cdot \log F_i\right) \qquad \text{equation (1)}$$

Where D = Shannon index, and F = the fraction of biomass of species i the vegetation. This diversity index will yield the value 0 when one species is present and the value of 1.0 when 10 species are present each having 10% of the biomass. The mean diversity index out of three runs is taken as a measure for final evaluation.

Results

Testing the effect of model simplification

In Table 5 the results of the simulations with the new, simplified model VEGPOP2 can be compared with the results of VEGPOP1 (Chapter 4) and with the measurements of Chapter 5. From this table it can be concluded that the simulated results of VEGPOP2 resemble to a large extent both the experimental results and the simulation of VEGPOP 1.

Field experiment:

In the nutrient-poor treatment the first year species adapted to moderately rich conditions were dominating whereas species adapted to nutrient-poor habitats performed worse (Figure 2). This was especially caused by *Plantago* which germinated early, had a relatively large seed mass and a high germination rate (field observation). After the second year perennials from a nutrient-rich habitat extended their dominance at the cost of the annuals and *Plantago*. In the same period perennials from a nutrient-poor habitat increased their abundance, which resulted in a total loss of annuals after two years of growing. The final year *Holcus* and *Rumex* stayed at the same level whereas especially *Festuca* increased its abundance at the cost of *Plantago* which continued to decrease.

Table 5. Biomass comparison (g shoot per pot at 1 october) between experimental results of Schippers et al. 1999 and simulations of different model versions simulating this experiment in the treatment where three species (*Holcus lanatus, Anthoxanthum odoratum* and *Festuca ovina*) were competing with each other.

	1995			1996		
	Holcus	*Anthox.*	*Festuca*	*Holcus*	*Anthox.*	*Festuca*
Low Nutrients (no nutrient application)						
Experiment	1.21	0.35	0.15	1.27	0.40	0.61
Full Model (VEGPOP 1)	1.12	0.35	0.17	1.30	0.15	0.52
Simplified Model (VEGPOP 2)	1.31	0.39	0.20	1.28	0.13	0.76
High Nutrient (application of 20gN m^{-2})						
Experiment	25.8	2.5	0.0	24.1	2.9	0.30
Full Model (VEGPOP 1)	18.2	0.23	0.2	20.2	0.0	0.02
Simplified Model (VEGPOP 2)	14.4	0.58	0.3	23.5	0.0	0.13

In the nutrient-rich treatment the relative abundance after the first year was almost the same as in the nutrient-poor treatment; only the species adapted to a low nutrient availability performed worse. In the second year 80% of the biomass that originated from perennial species adapted to the nutrient-rich habitat while after 3 years this group dominated 96% of the total biomass leaving only 2% for both annuals and *Plantago*. Species from a nutrient-poor environment had disappeared by then.

Simulating the field experiment

Figure 2 depicts the comparison between simulations with the full model and the field experiment. We see that especially the growth during the first growing season caused the difference between simulated and measured results. This was due to different germination success among the species in the experiment (*Poa, Holcus, Rumex, Anthoxanthum* were badly germinating whereas *Plantago* was a very good germinator) whereas in the simulations all fifty seeds of each species germinated. However, when the dynamics of different species groups are compared similarities between experimental and field results can be seen.

In the nutrient-poor treatment of both the simulation and the

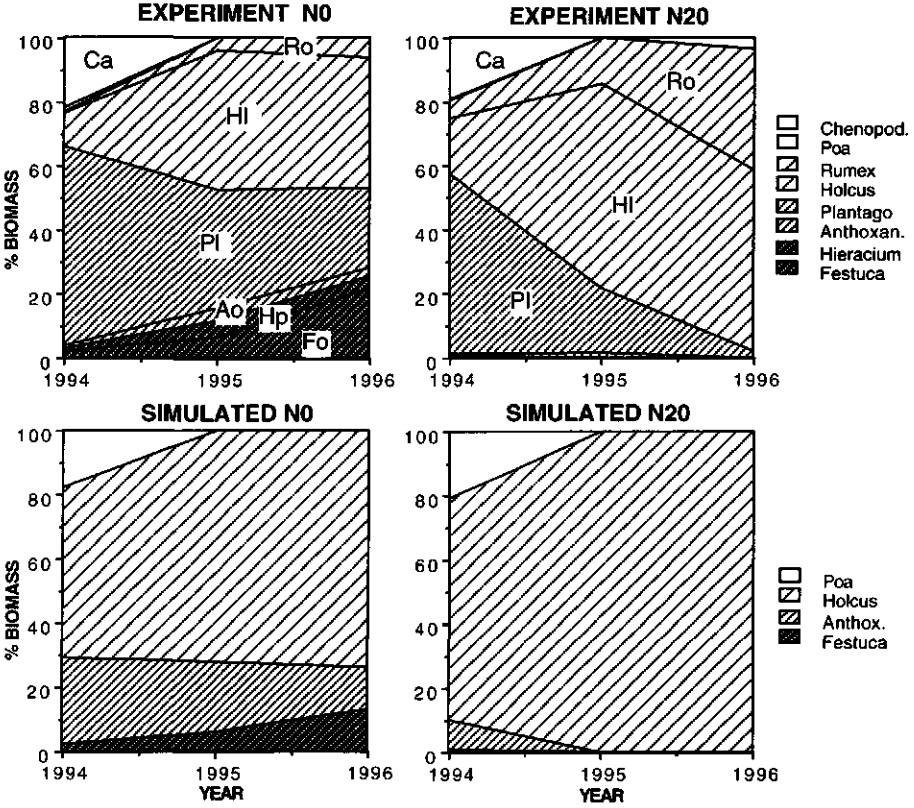

Figure 2. Modelled and experimental results of the competition between four plant groups at high and low nutrient level on sandy soil. White area represents annuals, light shaded area represents perennials of nutrient rich grasslands, dark shaded area represents species of nutrient poor grasslands and intermediate shaded area represents species from intermediate habitats. N0 = no nutrient gift, N20 = a nutrient gift of 20 gN m^{-2}.

experiment, annuals disappeared within one year. The perennials adapted to a nutrient-rich environment increased their dominance from the first to the second year and stayed steady from the second to the third year. Species from a moderately fertile environment decreased through the years in both the experiment and the simulation whereas species of nutrient-poor habitats showed a steady increase.

In the nutrient-rich treatment annuals decreased in the first year both in the simulation and the experiment and did not play an important role afterwards. Species from fertile habitats such as *Holcus* increased strongly in both the experiment and the simulation and excluded nearly all other species after 3 years. Species from moderately nutrient-rich habitats decreased in the experiment and the simulation whereas species from nutrient-poor habitat could not reach an abundance of more than 1% and were excluded after the second year in both the experiment and the simulation.

Scenario analysis: nitrogen and disturbance

In the 'mowing and removal' simulations, *Holcus* was prolific at all levels of disturbance and nitrogen load with the exception of 100% disturbance (Figure 3). *Anthoxanthum* and *Festuca* however, only survived at low levels of disturbance and nitrogen load. *Poa* profited from the increase of disturbance, and excluded all other species in the 100% disturbance level. As a consequence the diversity index reached the highest level at low levels of disturbance and low nitrogen loads whereas with the increase of both parameters the diversity decreased gradually.

When the cuttings were not removed, surprisingly, *Anthoxanthum* increased its dominance at low levels of disturbance at the cost of both other perennials. Compared to the 'mowing and removal' treatment the diversity index decreased especially at low levels of disturbance and nutrient load.

When the vegetation was not mown at all, *Anthoxanthum* disappeared completely, giving way especially to *Holcus*. *Festuca,* however, could maintain itself at zero nitrogen load at several levels of disturbance. This treatment gave the lowest diversity of all mowing treatments, only in one disturbance/nitrogen combination reaching a diversity values higher than 0.2.

Scenario analysis: nitrogen and boundary width

Figure 4 depicts the effect of boundary width and nitrogen load when there was no disturbance. At low levels of disturbance.these simulations largely confirmed the results of Figure 3 which means that the effect of boundary width was rather limited. Only when the width was 0.16 meter the diversity showed some reduction in the treatments that were mown. In the treatments without mowing, *Festuca* was able to maintain itself when the width was 2 meters at low nitrogen levels.

When the nitrogen application was distributed as a gradient, there was

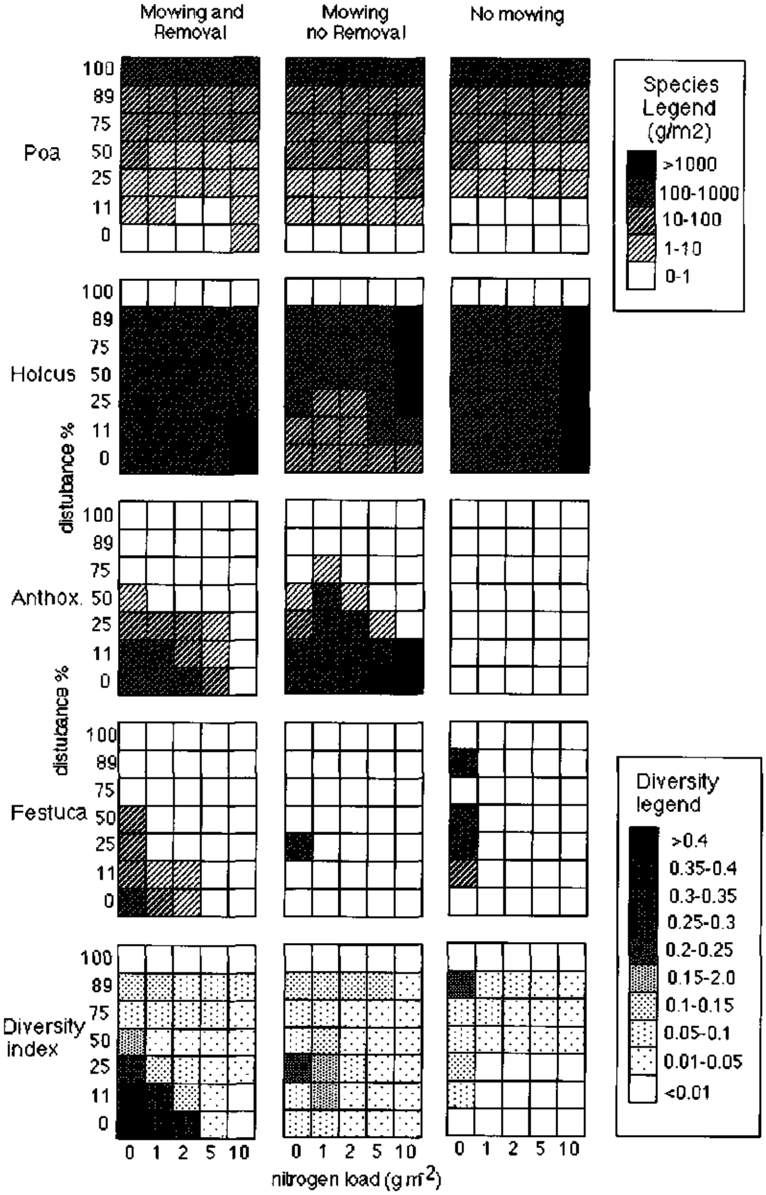

Figure 3. Simulated effects of nitrogen load and disturbance on the abundance of four species (*Poa annua*, *Holcus lanatus*, *Anthoxanthum odoratum*, *Festuca ovina*) in a field boundary vegetation after 10 years of growing. The model was parameterized with sandy soil data while Dutch weather conditions of 1985-1994 were used. The diversity index is according to Shannon & Weaver (1949).

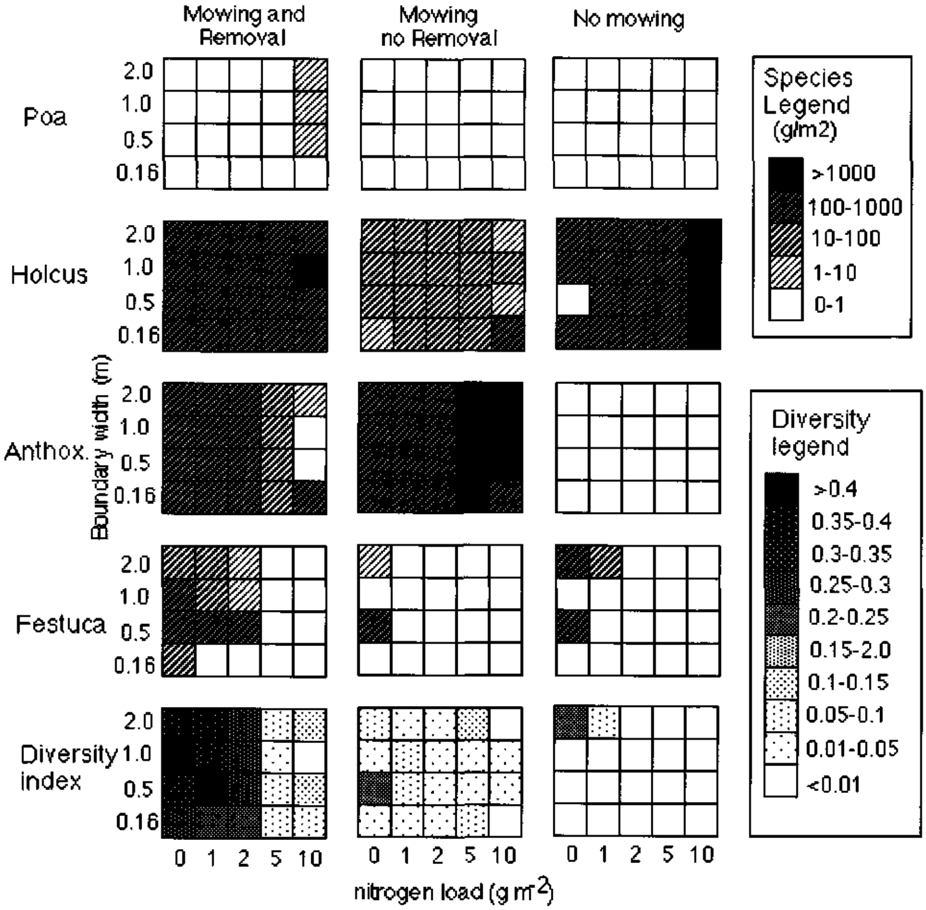

Figure 4. Simulated effects of nitrogen load and boundary width on the abundance of four species (*Poa annua*, *Holcus lanatus*, *Anthoxanthum odoratum*, *Festuca ovina*) in a field boundary vegetation after 10 years of growing. The model was parameterized with sandy soil data while Dutch weather conditions of 1985-1994 were used. The diversity index is according to Shannon & Weaver (1949).

an marked effect of the size of the boundary on the diversity (Figure 5). Especially *Festuca* profited from the increased boundary width and when the boundary width was 2 meters it was still present at the highest nitrogen level of 10 (note the nutrient load of the whole boundary in this case is comparable to a nutrient load of 5 g m^{-2} in the homogeneous case). In all mowing treatments, the richest biodiversity occurred at the lowest nutrient level at the widest boundary.

Discussion

Evaluating the approach

When performing any model study it is important to bear in mind the simplifications that have been made. Here, a major simplification is the omission of a water balance that affect growth directly. This limits the validity of the model to vegetation types in which water shortage does not play a key role.

A model as presented here is rather complex. It integrates a variety of processes and demands many parameters. This brings about uncertainty since parameters are not always known and all processes can not be precisely described. However, parts of the model had already been evaluated giving satisfactory results (Chapters 4, 5 & 6). Furthermore simulations of the VEGPOP2 model resembled the results of the experiment of Chapter 3 and the field experiment presented in this paper. These results confirmed the ability of VEGPOP2 to describe the complex vegetation dynamics and indicate the potential of this kind of approach for the evaluation of vegetation dynamics in general.

Another point of discussion is the evaluation of diversity with only four species whereas in real vegetations this number is often higher.A high diversity index in the model mean that *Festuca, Anthoxanthum* and *Holcus* were coexisting for 10 years producing in each of the three simulations considerable amounts of biomass. Giving the fact that these species are very different with respect to nutrient and disturbance tolerance, a high diversity index means that the environment is tolerant for very contrasting species and is likely also tolerant for other species as shown in the experiment.

Effect of nitrogen load

Current theory predicts that diversity is richest at intermediate productivity

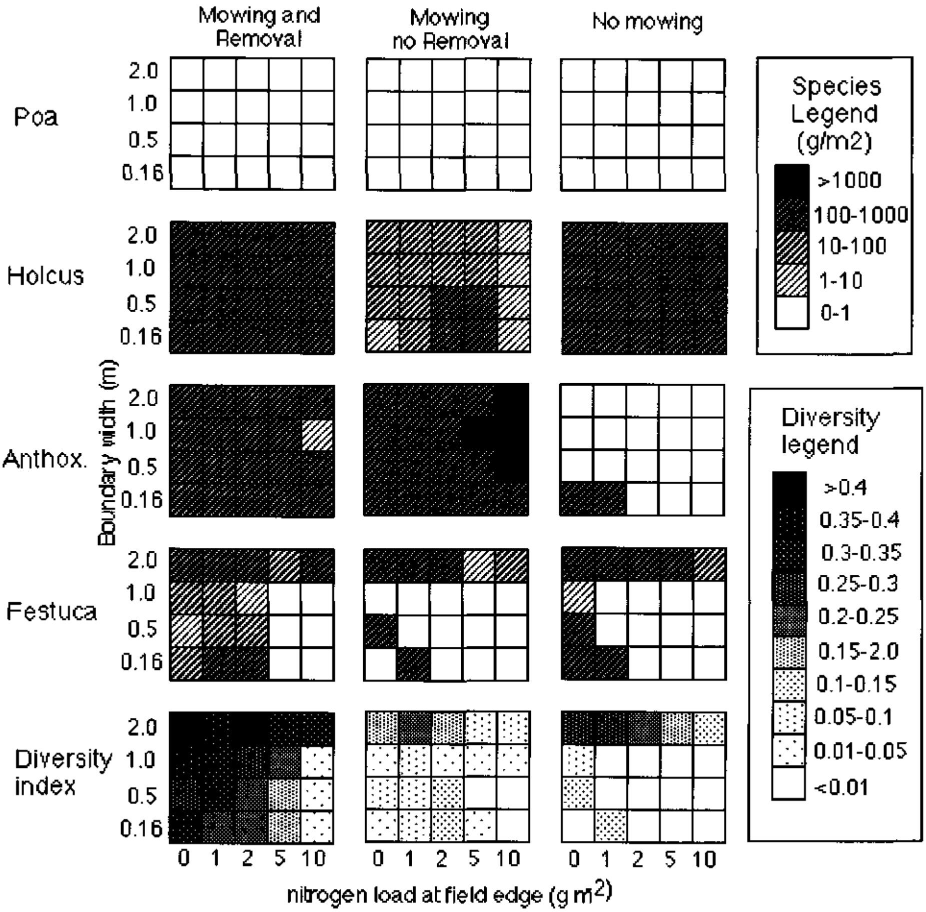

Figure 5. Simulated effects of nitrogen load, distributed as a gradient, and boundary width on the abundance of 4 species (*Poa annua*, *Holcus lanatus*, *Anthoxanthum odoratum*, *Festuca ovina*) in a field boundary vegetation after 10 years of growing. The model was parameterized with sandy soil data while Dutch weather conditions of 1985-1994 were used. The diversity index is according to Shannon & Weaver (1949).

levels of around 500g m^{-2} (Grime 1979). Since the productivity of arable field boundary vegetation is mostly above this level, the input of more nutrients is supposed to reduce species diversity in field boundaries (Kleijn 1997). This view is supported by our experimental results and simulations. In the nutrient-rich treatment of the experiment 6 out of 8 species were almost disappeared within 3 years whereas in the nutrient-poor treatment all perennial species were still present at that time. These results were also confirmed by the simulations. In all scenarios the maximum diversity was reached when there was no N input whereas the diversity index was reduced when the N load increased. Furthermore, simulation results indicate that even a small amount of fertilizer deposition already leads to a serious drop in the diversity index. It can therefore be concluded if a species rich field boundary vegetation is the objective nutrient input from arable field should be prevented.

Effects of disturbance

Results showed that the species with dormant seeds profited from the disturbance in spring. *Holcus* was able to suppress the growth of *Poa* until very high levels of disturbance. This result is partly in contradiction with the simulation results described in Chapter 5 where perennial species were out competed by annuals when more than 20% of the area was disturbed. In their model, however, perennial and annual adults where equally competitive whereas in this model, because of its taller architecture, *Holcus* was out performing *Poa* in disturbed cells. It is likely that taller annuals might be able to suppress *Holcus* at higher levels of disturbance.

Model results presented here, and the experimental work of Wilson & Tilman (1991) predict that high levels of disturbance will facilitates annuals. Annuals in an arable vegetation, however, are often weedy species. A boundary vegetation dominated by weeds is not preferable from a farmer's point of view since the boundary may function as a weed source. To prevent the development of a weedy vegetation the disturbance level must be relatively low to maintain a perennial vegetation. Simulations presented here and simulation of Chapter 5 indicate that in the long run disturbance levels lower than 20% prevent growth of annuals and may facilitate a diverse perennial vegetation.

Effect of boundary width

General theory concerning diversity-area relations predicts that diversity will increase with the inspected area (Williams 1964). For a field boundary vegetation this implies that a larger boundary width will support richer diversity on the landscape level because the amount of semi-natural vegetation increases. When this relation is an important factor explaining the simulation results we would expect an increase of the diversity in wider boundaries when the nitrogen was added homogeneously. Simulation results indicate, however, that the width-diversity effect was very limited (Figure 4). This could be explained by the low number of species and the relatively small area used in the simulations.

When the nitrogen load was distributed as gradient, boundary dimensions were more important. This can be attributed largely to the fact that, vulnerable species such as *Festuca* have the opportunity to escape from large N deposition. Hence the diversity in the simulations was largest at a boundary width of 2 meter where there still was a strip with very low load even at high nutrient deposition.

But what boundary width should be chosen to allow species to escape from nutrient load? This strongly depends on the accuracy of fertilizer broadcasters and the precautions taken by the farmer to prevent fertilizer misplacement. Research of Melman & Van der Linden (1988) and Rew et al. (1992) shows that different types of spreaders give variable results, but that especially the frequently used twin disc and oscillation spout broadcasters are not capable to create a very steep fertilizer gradient. This means that farmers will loose yield in order to protect the boundary or will spoil fertilizer on the boundary to keep maximum yield.

In general it can be stated that wide boundaries have richer diversity for two reasons: 1)They provide the opportunity of escape from large nutrient input and 2) species numbers increase with increasing area. Therefore, it can be concluded that the boundary width-diversity relation of a boundary in certain area is strongly determined by the local fertilizer misplacement curve and the local relation between area and plant species diversity.

Effect of mowing

Mowing and removal is considered a way to increase species diversity in grassland communities for three reasons: 1) it generates a large loss of nutrients from the ecosystem, 2) it reduces competition for light and 3) it levels off competitive differences between species because tall, dominant species encounter the largest biomass losses due to mowing (Bakker 1989, Berendse et al. 1992). In general our simulations confirm this view, but an unexpected result was the increased dominance of *Anthoxanthum* over *Holcus* when cuttings were not removed. One would expect species from more nutrient-rich soils to be more competitive in this condition because nutrients from cuttings increase soil fertility. An explanation for this unexpected effect is found in the timing of nutrient release from the cuttings. The (model) vegetation was mown in September when *Holcus* is much taller than *Anthoxanthum,* and therefore loses a larger part of its above ground biomass compared to *Anthoxanthum*. This was not crucial in the 'mowing and removal' treatment since there was a low nutrient availability after the mowing period. However, when the cuttings were not removed a nitrogen flush followed the mowing which supported especially the the growth of the less damaged *Anthoxanthum.*

Simulation results indicate that the omitting of mowing resulted in low disturbance levels mostly in a monoculture of *Holcus* and resulted in the lowest diversity compared to the other treatments.

8

General discussion

The study of plant competition processes described in this thesis and summarized in a model used to answer questions about field boundary management has yielded recommendations for field boundary management and conclusions that are relevant for plant ecology theory. The general discussion, therefore, is divided into two parts that deal with each of these aspects. Since most topics have already been discussed in previous chapters, this chapter largely focuses on further research.

Recommendations for field boundary management

Recall that Chapter 7 resulted in the following advice on measures to be taken to enhance the diversity of the field boundary vegetation:

1) Avoid all nutrient inputs from the arable field.
2) Mow and remove the mown material.
3) Restrict the disturbance level to less than 20% of the area per year.
4) Keep the boundary as wide as possible, but at least wider than the maximum fertilizer drift.

The high nutrient inputs in the field boundary can be considered as one of the most important problems in field boundary managements (conclusion 1). The research described in this thesis confirmed that large nutrient inputs induce high competitive asymmetry between species, which brings about a vegetation with little diversity. It would be easy to solve this problem by improving the accuracy of fertilizer broadcasting equipment. Good progress has already been made with pneumatic broadcasters which have a precision in the order of decimeters (Kleijn 1997). Growing interest in precision farming makes it likely that equipment will become even more accurate in the future.

Conclusion 2 that mowing enhances biodiversity, is based not only on the disproportional effect of mowing on the taller, in principle superior species. When the mowings are removed, mowing is also an important remover of nutrients. This extra loss is useful in conditions where boundaries are too rich in nutrients, which is generally the case.

To prevent weeds (annuals) from establishing in the field boundaries and becoming a source of weed seeds for the arable field, disturbance in the arable field boundaries must be kept below 20% of the area per year (conclusion 3). This can be achieved by avoiding the use of heavy machinery in the boundaries and by not spot-spraying with broad spectrum herbicides (De Snoo 1995). The results presented in Chapter 7 indicate that mowing and removal may be a better strategy to get rid of annual weeds than spot application of herbicides.

In general, it can be stated that wide boundaries support diversity for two reasons (conclusion 4): 1) Some vegetation is able to escape large nutrient inputs and 2) the larger semi-natural area in the agricultural landscape provides space for more species, in accordance with the species-area relationship. Increasing the boundary width has serious economic consequences for the farmer, however, because it reduces the productive area. It is therefore important to quantify the boundary width-diversity relation which may be obtained from the local species-area relation. Such a relationship can predict the short-term diversity potential of an increase in width. To estimate the effect of increasing the boundary width on the biodiversity in the long run, diversity area relations should be estimated in landscapes on similar soils with different areas of field boundary per hectare. When the local boundary width-diversity relation is determined, the biodiversity potential of a chosen boundary width can be related to the loss of productive area.

Another factor that should determine decisions about the boundary width, is the accuracy of the fertilizer broadcasters used. When equipment is inaccurate, narrow boundaries will always have a low diversity. Therefore the boundary should be wide and a considerable amount of arable field has to be sacrificed. This is particularly important because one full fertilizer dose in the boundary may already cause a serious species loss (Chapter 7). It might be a good idea to relate the width of the boundary to the precision of the fertilizer broadcaster used by the farmer.

Biodiversity of the field boundary: further research

The major conclusions of this study are based on local dynamics considering vegetation at the scale of a square meter level. Although we incorporated dispersal and establishment in the models, these processes were only used to simulate local dynamics of the species present (Chapters 5 & 7). Hence this study focused mainly on coexistence, competitive asymmetry and survival aspects. From a meta-population point of view, however, the biodiversity is also determined by the colonization (Levins 1969, 1979). Although the meta-population aspect is ignored in this study, it is clear that the simulation tools developed would help elucidate meta-population dynamics. The TRANSPOP and VEGPOP models can handle multiple species and incorporate dispersal, establishment and extinction in a spatially explicit environment. Additionally, SEEDTRIP is able to generate seed shadows. These are all necessary ingredients for a good meta-population study, and I think that the logical follow-up to this thesis would be a meta-population study to assess the rate of recolonization of species with various life history strategies in field boundaries.

Another interesting step might be the optimization of mowing management. VEGPOP2 is able to handle various mowing regimes which may vary in time, frequency and height. Simulations with this model might generate hypotheses about optimal mowing regimes with respect to diversity in various grassland communities.

Plant ecology theory: main conclusions

1) Species adapted to nutrient-rich environments are characterized by a tall specific shoot height and a large specific leaf area, whereas species adapted to nutrient-poor habitats are characterized by low biomass turnover (Chapters 2 & 4).

2) At low nutrient levels, winter is the crucial period determining plant competition (Chapter 3).

3) Competitive asymmetry increases with nutrient supply (Chapters 3 & 4).

4) Perennial competition can be simulated on the basis of eco-physiological and morphological principles (Chapter 4).

5) Spatially explicit models are necessary when vegetation processes are simulated (Chapter 4).

6) Competitive responses reduce competitive asymmetry between species and may facilitate coexistence between species that have approximately the same competitive ability (Chapter 3).

7) Stable coexistence may occur along a range of disturbance levels between species with dormant and non-dormant strategies having the same adult longevity (Chapter 5).

8) With increasing disturbance, respectively non-dormant perennials, dormant perennials, non-dormant annuals and dormant annuals became dominant, indicating the relative viability of these particular strategies with respect to disturbance (Chapter 5).

9) The simulation model of Andersen (1991) can be regarded as useful for the estimation of seed shadows generated by wind in herbaceous species (Chapter 6).

10) The dropping method and the floating method are both appropriate for estimating terminal velocities of seeds in herbaceous species (Chapter 6).

Plant ecology theory: further research

Species properties

This study confirms the view of Grime (1979), Berendse & Elberse (1990), that specific leaf area, specific shoot height and tissue longevity are the crucial plant characteristics that determine to what extent herbaceous species can adapt to the nutrient availability of their habitats (conclusion 1). It can also be concluded that grassland species from a nutrient-poor environment take marked advantage of their lower tissue turnover in winter (conclusion 2). This study showed that perennial species such as *Holcus lanatus* and *Anthoxanthum odoratum* experience serious losses during a severe winter. Although most plants were able to recover, it raises the question whether a strict perennial-annual system is useful as many annual species are also able to survive mild winters. Given that winter is such a crucial period in plant competition it may be a good idea to define a more quantitative scale of winter survival for grassland species than is used at present.

Our results and those of others show that turnover is as important as growth in perennial species in nutrient-poor environments. However, there have been many short-term studies that only considered plant growth. More experimental studies (for instance in climate chambers) of tissue-turnover and longevity would lead to better understanding of this process and would improve our understanding of the vegetation dynamics.

Competitive asymmetry
Our results contradict the view of Newman (1973), Grubb (1985) and Tilman (1988) and support the view of Grime (1979) and Keddy (1989) that competitive asymmetry increases with nutrient supply (conclusion 3). There are two factors that cause the enhancement of competitive asymmetry at greater nutrient availability: first, the increase of lateral spread of a species reduces patchiness and enhances competitive interactions; second, the increase of nutrient availability induces more light-limited growing conditions and light is a more disproportional resource than nutrients (Chapter 4). Although the vertical aspects of competition are well understood (Kropff & Van Laar 1993) the effect of lateral expansion on the competitive asymmetry has not been well studied. Further study on the importance of horizontal spread on species interaction may improve our understanding of the role of horizontal spread in the interspecies competition in grassland systems.

The competitive response is the change of species properties when subjected to competition with other species. This means that subordinate species become more competitive as a result of the environmental change brought about by the dominant species. Subordinate species encounter a higher air humidity, less light and less wind. They, therefore, respond with thinner leaves and stems which increases their efficiency (Kropff & Van Laar 1993). This process may be crucial in the reduction of competitive asymmetry between species and might even cause coexistence among species with similar properties (conclusion 6).

Although plasticity of species has generally been well studied (e.g. Rice & Bazzaz 1989, Aerts & De Caluwe 1994, Van Tienderen & Van Hinsberg 1996, Robinson & Van Vuuren) its function in the coexistence of species and the maintenance of diversity has been neglected. Replacement design studies in combination with the use of competition models might give more insight into the importance of this process in the reduction of competitive asymmetry. Competition models such as VEGPOP can predict how plastic a subordinate plant must be to survive competition, whereas competition experiments can be used to verify of such predictions.

Plant strategies and disturbance

In Chapter 5, coexistence was found between species with non-dormant and dormant seeds with the same adult longevity (conclusion 7) which can be regarded as escape in time. Escape in space and time are generally well known phenomena (Venable & Lawlor 1980). Although spatially explicit models have shown that superior competitors that leave empty spaces in the community coexist with good dispersers that can colonize such spaces rapidly, stable coexistence between species that have dormant and non-dormant seeds had not previously been reported and escape in time can be regarded as a new mechanism allowing coexistence between species.

Plants will only profit from escape in time or space when the conditions for growth and establishment are better later in time or elsewhere. In our model, coexistence between species with dormant and non-dormant seeds can be explained by the fact that strategies with dormant seed were able to establish in disturbed patches which appear later.

Simulations with the TRANSPOP model predicted that with the increase of disturbance level, non-dormant perennials, dormant perennials, non-dormant annuals and dormant annuals predominate in that sequence, indicating the relative viability of these particular strategies with respect to disturbance (conclusion 8). Although this hypothesis is partly confirmed by the data set of Grime et al. (1988) these predictions need more experimental confirmation.

Another hypothesis induced by the TRANSPOP simulations was that plants are expected to optimize their seed size in such a way that they maximize their competitive ability (W_i) per unit of invested seed biomass. In other words, when a plant invests 1 gram in seeds it is more effective to produce 1000 seed of 1 mg than 100 seeds of 10 mg if each seed has an equal chance of becoming an adult. This immediately raises the question of what the W_i-seed mass curve looks like. Studies with plant competition models such as VEGPOP that include numbers and biomass may generate testable predictions about this relation.

Dispersal

Measurements of seed dispersal by wind are generally difficult because they are influenced by fickle weather conditions. This means that an experiment in the field will not yield generalizable results but will only reflect the dispersal of a species during the experimental period, which is unlikely to represent dispersal in general weather conditions.

Another problem is the assessment of the tail of the seed shadow. Field experiments cannot assess the tail of seed shadow curves because of the low probabilities of seed arrival in the tail of the curves and the large catchment area needed at larger distances. These problems could be overcome with good explanatory models to describe the wind dispersal process. The model of Andersen (1991), tested in this thesis, is a good candidate for the assessment of seed shadows generated by wind (conclusion 9). The model was able to simulate seed shadows generated in the wind tunnel experiment and gave good results in a field experiment (Andersen 1991). Combining this model with long-term wind data and realistic terminal velocities can be considered an important step forward in the assessment of seed shadow curves, as was shown in Chapter 7.

The results of Chapter 6 indicate that a simple vertical wind tunnel is a good alternative for the dropping method to assess terminal velocity values of herbaceous seeds (conclusion 10).

Modelling the dynamics of plant communities

This study has shown that spatially explicit models are necessary when vegetation processes are simulated (conclusion 5). Two spatially explicit models were developed, which can be used to study various aspects of the vegetation dynamics.

In Chapter 5, we developed a new model, TRANSPOP, that simulates the population dynamics of various species/strategies in a spatially explicit environment. We used the model to investigate the effect of disturbance on the competition between eight life history strategies. But there are still various questions that might be answered using this model.

- When we add clonal reproduction to various strategies questions can be answered about the trade-off between investment in seeds and investment in clonal reproduction such as stolons.
- In Chapter 5, we only used random disturbance patterns of one cell size. How would the eight life history strategies as studied in Chapter 5 respond to other (e.g. more patchy) disturbance patterns?
- Adding more realistic seed shadows (e.g. from SEEDTRIP) and different habitat qualities to the TRANSPOP model may answer questions about meso-scale meta-population dynamics.
- Predictions that r and K strategies could coexist (Fagerström & Ågren 1979, Hastings 1980, Tilman 1994) were obtained with spatial models using

single difference equations that did not incorporate dormancy. Would the same results be obtained with models such as TRANSPOP that separate processes in time and allow dormancy?

Results of the VEGPOP models showed that perennial competition can be simulated based upon eco-physiological and morphological principles (conclusion 4). From this it can be concluded that the model VEGPOP is a suitable tool for investigating eco-physiological and morphological strategies. For instance, the research presented here underlines the importance of regrowth in spring and after mowing, in the competition between perennial species. Sensitivity analysis of the grasses showed that reallocation of reserves is not an important factor in the competition between grass species (Chapters 4 & 7). Many species, however, have large storage organs. For instance *Rumex obtusifolius* had stored up to 60% of its total biomass production in its taproot (Chapter 2). This raises the question of how plants should optimize their allocation, given the risk of defoliation in summer and winter. VEGPOP might be a valuable tool for generating hypotheses about how plants should optimize their reserve allocation.

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Summary

The Dutch field boundary, usually a strip of semi-natural grassland bordering arable fields, can be considered as an important area for the survival of plant species in landscapes dominated by agriculture. The intensification of agriculture in recent decades has led to a decline in the natural plant diversity in many agricultural landscapes. The specific developments responsible fore the reduction of plant biodiversity are: 1) the increase of fertilizer use 2) the increase of disturbance, 3) the change in mowing regime, and 4) the reduction of field boundary area.

To evaluate of the effect of the various factors on the vegetation dynamics in field boundary communities experimentally, a large and long-term experiment should be carried out. Suitable simulation models, however, could give a quick insight into the effects of various factors on field boundary communities. Therefore, we developed a new model (VEGPOP2) that comprises the processes and factors that determine the dynamics of the field boundary. This main model was used to answer the central question of this thesis as formulated in Chapter 7: what are the effects of nitrogen load, artificial disturbance, boundary width and mowing regime on the composition and dynamics of the field boundary vegetation?

The main model, described in Chapter 7, is the result of the integration of three new simulation models as described in Chapters 4, 5 and 6: a plant competition model VEGPOP1 (Chapter 4), a seed dispersal model SEEDTRIP (Chapter 6) and a spatial population dynamical model TRANSPOP (Chapter 5). Experimental results presented in Chapters 2, 3, 5, 6 and 7 of this thesis were used to provide parameters for the models and to produce data to evaluate the models.

Four grassland species were selected and used in most simulations and experiments: *Poa annua* L. representing an annual species from disturbed nutrient-rich habitats, *Holcus lanatus* L. representing a perennial species from nutrient-rich habitats, *Anthoxanthum odoratum* L. representing perennial species from moderately fertile habitats and *Festuca ovina* L. representing perennial species from nutrient-poor habitats.

In chapter 2, the results of a pot experiment are presented in which species characteristics of eight grassland species were related to the fertility of

their habitat. Species from a nutrient-rich habitat were characterized by a larger specific leaf area and taller specific shoot height (height/shoot biomass), resulting in a higher relative growth rate and total biomass in all nutrient conditions. There was no evidence that species from nutrient-poor environments had superior growth characteristics at low nutrient levels. The only advantage displayed by these species was a lower leaf turnover.

Chapter 3, considers the role of seasonal change, plasticity induced by competition response and nutrient availability in the competitive relations of three grassland species. on the basis of a competition experiment conducted using three perennial grasses from habitats with different nutrient availabilities. Three key traits determining the successional status of the species were studied: specific leaf area, specific shoot height and the fraction of dead leaves. Response of these traits to competition appeared to be limited and insufficient to change the competitive relations in the experiment. All three traits showed marked seasonal changes, which resulted in a change in competitive ability during winter in favour of the species adapted to nutrient-poor environments. Furter results support the theory that competitive asymmetry increases at higher nutrient levels. It is postulated that the directionality of light makes it possible for the dominant species to monopolize this resource more easily than nutrients.

In Chapter 4, the competition among perennial grassland species is analysed. A spatially explicit plant competition model VEGPOP1 is developed for this purpose and used to answer the following questions: Can complex perennial competition processes be simulated accurately based on eco-physiological principles? What are the crucial parameters and processes determining interspecies competition? How does spatial heterogeneity affect competition for light and nitrogen between the species? The model was parameterized using experimental data from Chapters 2 and 3. Various simulations were performed to answer the above questions. The model was able to simulate complex perennial competition processes as observed in the experiment presented in Chapter 3, which indicates that it has potential for analysing vegetation succession. Simulations with a spatially explicit version of the model showed that patchiness of the species distribution causes a reduction of competitive asymmetry, especially under nutrient-poor conditions; from this is concluded that, when complex vegetation processes are studied, space should be incorporated in the model. The model's great sensitivity to plant height, specific leaf area and biomass turnover, and the large interspecies differences indicated that these are the key parameters determining competition between the species studied. The low shoot turnover of *Festuca* was responsible for survival during winter and enabled this species to have a better start in spring, resulting in an unexpected comeback after winter in the second year.

Chapter 5 describes a model study performed to examine the importance of adult longevity, seed longevity and seed size in relation to environmental disturbance. Eight plant strategies were defined by permutating a high value and low value of each of the three traits, taking trade-offs into account. A simple, spatially explicit model (TRANSPOP) was developed that simulated the population dynamics of plants exhibiting the eight strategies at different levels of disturbance. With increasing degree of disturbance, non-dormant perennials, dormant perennials, non-dormant annuals and dormant annuals became dominant, in that sequence, indicating the relative viability of these particular strategies with respect to disturbance. When the disturbed area was less than 20% (y^{-1}), perennial species excluded annuals, but at greater disturbance the annuals were more successful. A new prediction from the model was that coexistence can occur between species with dormant and non-dormant seeds with otherwise identical traits.

To obtain realistic seed dispersal curves a promising individual-based model for seed dispersal (SEEDTRIP) was tested for different wind velocities and for a variety of seeds (Chapter 6). Simulation results from the seed dispersal model were compared with observations in a horizontal wind tunnel. Taking the large variation in seed morphology and seed mass into account, the simulation results fitted the wind tunnel results reasonably well, indicating the general applicability of the model for herbaceous species.

The terminal velocity of seeds, the crucial species-specific parameter of SEEDTRIP model, can be assessed by two methods: a dropping method and a method to float seeds in an upward air stream. Chapter 6 presents V_t-values determined with both methods. This experiment shows that a simple vertical wind tunnel can be regarded as a good alternative to the dropping method for assessing terminal velocity values of herbaceous species.

In Chapter 7, the main questions of this thesis is broached: what are the effects of fertilizer load, disturbance, mowing and boundary width on the field boundary vegetation? To answer this question a new model, VEGPOP2, was developed that comprises the mechanisms described in the previous models. The new model incorporates competition for nitrogen and light as well as mineralization, population dynamics and seed dispersal.

The model was parameterized for four grasses using data from the preceding chapters. To test the model, simulation results were compared with the results of the pot experiment described in Chapter 3 and a new field experiment. Several long-term simulations (10 years) were performed to analyse the effect of various factors on the field boundary composition.

The results of the model were generally in agreement with the results of the experiment. The simulation study indicated optimal coexistence of perennials when nutrient input and disturbance were low, the mown material was removed and the boundary was wide. The conclusion is that the perennial diversity of the field boundary vegetation is promoted by four measures: 1) prohibiting all nutrient inputs from the arable field, 2) keeping the disturbance level under 20% of the area (y^{-1}), 3) mowing and removing the mown material, and 4) keeping the boundary as wide as possible but at at least wider than maximum fertilizer drift.

Chapter 8, the general discussion, is divided into two parts: first, the implications of the main conclusions for field boundary management are discussed, followed by a discussion of the main conclusions for the general plant ecology of grasslands in the temperate zone.

Samenvatting

De akkerzoom, in Nederland vaak een strook semi-natuurlijk grasland naast de akker, kan gezien worden als belangrijk voor de overleving van plantensoorten in landschappen die worden gedomineerd door de landbouw. Als gevolg van de intensivering van de landbouw is in de afgelopen decennia het aantal plantensoorten in deze landschappen sterk afgenomen. Verschillende oorzaken kunnen hebben geleid tot de afname van de plant diversiteit in de akkerzoom: 1) toename in het gebruik van meststoffen, 2) toename van verstoringdruk, 3) veranderingen in het maairegime en 4) de afname van het oppervlak van de akkerzoom.

Een groot en langdurig experiment zou nodig zijn om de invloed van de verschillende factoren experimenteel te analyseren. Geschikte simulatiemodellen kunnen daarentegen snel inzicht geven in het effect van verschillende factoren op de plantengemeenschappen in de akkerzoom. Daarom ontwikkelden we een nieuw model, VEGPOP2, dat processen en factoren die de dynamiek in de akkerzoom bepalen, simuleert. Dit centrale model werd gebruikt om de hoofdvragen, zoals geformuleerd in Hoofdstuk 7, te beantwoorden: Wat zijn effecten van nutriëntenbelasting, verstoringen, maairegime en akkerzoomafmetingen op de dynamiek en samenstelling van de akkerzoom?

Het centrale model zoals beschreven in Hoofdstuk 7 is het resultaat van het integreren van drie modellen die zijn beschreven in andere hoofdstukken: een concurrentiemodel VEGPOP1 (Hoofdstuk 4), een ruimtelijk expliciet populatiedynamisch model TRANSPOP (Hoofdstuk 5), een dispersiemodel voor zaden SEEDTRIP (Hoofdstuk 6). Experimentele resultaten uit Hoofdstukken 2, 3, 5, 6 en 7 werden gebruikt om de modellen te parameteriseren en te testen.

Vier grassen, uit habitats met verschillende nutriëntenbeschikbaarheid, werden gebruikt voor de simulaties en experimenten; Straatgras: *Poa annua* L. , Witbol: *Holcus lanatus* L., Reukgras: *Anthoxanthum odoratum* L. en Schapegras *Festuca ovina* L.

In Hoofdstuk 2 werden de resultaten van een potproef beschreven waarin de eigenschappen van acht graslandsoorten werden gerelateerd met de nutriëntenrijkdom van hun habitat. Soorten uit rijke milieus hadden een hoger specifiek bladoppervlak en waren relatief langer, wat, ongeacht de rijkdom van milieu, voor een snelle groei zorgde. Er werd geen bewijs gevonden dat soorten aangepast aan een arm habitat betere groeieigenschappen hadden bij lage nutriëntenbeschikbaarheid, wel hadden deze soorten een lagere bladsterfte.

In Hoofdstuk 3 werd de invloed van: seizoensveranderingen, plasticiteit en nutriëntenbeschikbaarheid op de concurrentie tussen graslandsoorten bestudeerd. Daarvoor werd een concurrentieexperiment uitgevoerd met drie perenne grassen afkomstig uit habitats met verschillende nutriëntenrijkdom. Drie sleuteleigenschappen werden bestudeerd: het specifieke bladoppervlak, de specifieke planthoogte en de bladsterfte. De plasticiteit van deze eigenschappen, geinduceerd door concurrentie, bleken niet voldoende om de concurrentieverhoudingen te veranderen. De drie eigenschappen vertoonde echter wel heftige schommelingen veroorzaakt door seizoensinvloeden. Verder onderschreven de resultaten de theorie dat concurrentie intensiteit toe neemt met de nutrient beschikbaarheid. Mogelijk komt dit doordat licht een duidelijke richting heeft en daardoor, vergeleken met nutriënten, makkelijker te monopoliseren is voor de langste plant.

In Hoofdstuk 4 werd de concurrentie tussen de graslandsoorten uit Hoofdstuk 3 geanalyseerd. Hiertoe werd een ruimtelijk expliciet plantconcurrentiemodel 'VEGPOP1' ontwikkeld. Modelresultaten werden gebruikt om de volgende vragen te beantwoorden: Kan een complex concurrentieproces worden gesimuleerd met behulp een eco-fysiologisch model? Welke parameters en processen bepalen de concurrentie? Wat is het effect van groepsgewijs groeien van soorten op de uitkomst van de concurrentie om licht en voedingsstoffen?

Gegevens uit de Hoofdstukken 2 en 3 werden gebruikt om het model te parameteriseren. Om de bovenstaande vragen te beantwoorden werden er verschillende simulaties uitgevoerd. Het model was in staat de complexe proef uit Hoofdstuk 3 te simuleren. Dit illustreert de mogelijkheden van dit soort modellen om vegetatieprocessen te beschrijven. Ruimtelijke expliciete simulaties lieten zien dat groepsgewijs groeien van soorten de concurrentie-intensiteit tussen soorten doet afnemen. Dit gebeurde vooral in arme omstandigheden. Verder liet de gevoeligheidsanalyse zien dat, net als in Hoofdstuk 2, de plantlengte, het specifieke bladoppervlak en de sterftesnelheid de belangrijkste parameters waren die de concurrentie bepaalden, omdat deze eigenschappen een hoge gevoeligheid in het model combineerden met grote soortsverschillen.

Een modelstudie naar het belang van levensduur van de volwassen plant, levensduur van het zaad en de zaadgrootte in relatie tot verstoring wordt beschreven in Hoofdstuk 5. Acht strategieën werden gedefinieerd door telkens hoge en lage (realistische) waarden van de drie planteigenschappen te combineren, waarbij rekening gehouden werd met de biomassabalans van de planten. Er werd een nieuw en simpel ruimtelijk expliciet populatiedynamisch model ontwikkeld waarin de acht strategieën met elkaar concurreerde bij verschillende verstoringsintensiteiten. Met de toename van de verstoring domineerden in de concurrentie respectievelijk: perenne soorten met kort levende zaden, perenne soorten met lang levende zaden, annuellen met kortlevende zaden en annuellen met langlevende zaden. Bij een verstoringsdruk van minder dan 20% per jaar waren perenne soorten in staat annuellen geheel te onderdrukken, terwijl boven de 20% het omgekeerde plaats vond. Het feit dat in het model soorten met langlevende zaden stabiel in evenwicht zijn met soorten met kortlevende zaden met verder gelijke eigenschappen kan als nieuw worden beschouwd.

Om inzicht te krijgen in het dispersie proces van zaden werd een dispersiemodel (SEEDTRIP) getest voor verschillende zaden en windsnelheden (Hoofdstuk 6). Dit werd gedaan door simulatieresultaten te vergelijken met dispersieobservaties in een horizontale windtunnel. Als we de grote variatie in de morfologie en het gewicht van de zaden in ogenschouw nemen komen simulatieresultaten goed overeen met de waarnemingen in de windtunnel wat aangeeft dat het model goed functioneert voor zaden van kruidachtige planten.

De terminale valsnelheid V_t, de belangrijkste soortsspecifieke parameter van het SEEDTRIP model, kan worden bepaald met twee methoden: een valmethode en een methode die zaden laten zweven in een opwaardse luchtstroom. De vergelijking tussen beide methoden (Hoofdstuk 6) laat zien dat een simpele verticale windtunnel net zulke goede resultaten geeft als de val methode om valsnelheden van zaden te bepalen.

In Hoofdstuk 7 werd de centrale vraag van dit proefschrift behandeld: wat zijn de effecten van kunstmest belasting, verstoring, maaien en breedte van de akkerzoom op de vegetatie van de akkerzoom? Om deze vraag te beantwoorden werd een model ontwikkeld dat beschouwd kan worden als een integratie van de modellen uit de voorafgaande hoofdstukken. Het nieuwe model omvat naast processen zoals concurrentie om licht en stikstof, ook mineralisatie, populatiedynamica en dispersie. Om het model te testen werd het geparameteriseerd voor 4 grassen en de simulaties vergeleken met het potexperiment uit Hoofdstuk 3 en met een nieuw veldexperiment. Om het effect van verschillende factoren op de samenstelling van de akkerzoom te analyseren werden een groot aantal lange termijn simulaties gedaan (10 jaar).

Simulatieresultaten kwamen in grote lijnen overeen met de experimentele resultaten. De grootste diversiteit van overjarige plantensoorten werd gevonden in simulaties waarbij de bemestingsdruk en de verstoringdruk laag waren, het maaisel afgevoerd werd en de breedte van de strook maximaal was. Daarom kan worden geconcludeerd dat diversiteit van overjarige planten in de akkerzoom kan worden bevorderd door: het vermijden van mestdepositie in de akkerzoom, het verstoringsniveau in de akkerzoom onder 20% per jaar te houden, te maaien en het maaisel af te voeren, de akkerrandstrook zo breed mogelijk te maken maar in iedergeval breder dan de maximale afstand van de mestdepositie.

Hoofdstuk 8, de algemene discussie, bestaat uit twee delen: het eerste deel behandelt de consequentie van de hoofdconclusies voor het akkerzoombeheer, terwijl het tweede deel de betekenis van de conclusies voor ecologie in het algemeen behandelt.

Nawoord

Het aardige van een proefschrift schrijven is dat je niet weet waar je aan begint omdat je het nooit eerder hebt gedaan. Je start heel optimistisch en denkt het wel in vier jaar te klaren. Het is nu zeven jaar later. Mijn motivatie in deze periode was vooral nieuwsgierigheid naar hoe ecosystemen werken en hoe deze op een elegante manier in modellen samen te vatten. Wel, ik ben aan mijn trekken gekomen!

De meeste werken van een zekere afmeting zijn aan meer dan één mens te danken. Dat is ook hier het geval. Ineke Snoeijing en Marein Verbeek hielpen bij het experimentele werk. Ineke, ik zie ons nog schapegrasjes splitsen in dode en levende sprietjes. De volgende keer neem ik een soort met grote bladeren. Mijn studenten, Ronneke Jansen en Eelke Jongejans, probeerden mijn begeleiderskwaliteiten uit, ik hoop dat het een beetje bevallen is. Wetenschappelijke discussie was er bij de 'boys': Leo Vleeshouwers, Corné Kempenaar, Eddy Kremer en Jacco Wallinga. De TPE-lunchcrew zorgde voor de broodnodige afleiding. Genoten heb ik van de populatiedynamica op woensdagavond met Jan van Groenendael en Leo Vleeshouwers (zie hoofdstuk 5). Onder mijn palm zat ik gezellig met mijn kamergenoten: David Kleijn, Jacaranda van Rheenen en Paula Westerman. Cor Langeveld, Annemarie van Dam en Reinout Seegers redden dagelijks de backup bandjes van branden, aardverschuivingen en diefstal. Rod Hunt, Joke Snel, Ilse Chang en Joy Burrough waren verantwoordelijk voor het gladstrijken van mijn soms wel erg gekreukelde engels. Gon van Laar wilde kleine kwadraatjes en subscriptjes, door haar ziet dit proefschrift er professioneler uit. Wouter Joenje sleepte het akkerrandenproject in de wacht en deed de begeleiding. De bazen, Martin Kropff en Frank Berendse waakten over de kwaliteit van dit proefschrift. Verder zorgde het onvolprezen BKK, de filosofen en het eetgroepje voor een afgesopte geest na daagjes gepieker. Marianne Withagen en Beppe pasten op Wike terwijl ik op het proefschrift paste. Thuis werd bevrouwd door Wike en Antke een, door dit proefschrift, soms wel ondankbare taak.

Bedankt allemaal!

Peter

Curriculum vitae

Peter Schippers was born in 1955 in Arnhem. He was graduated from Wageningen University (WU) in 1988. In 1989 he started a project on intraspecific taxonomy and population dynamics of Yellow Nutsedge (*Cyperus esculentus*) at the department of Plant ecology and Weed science (WU). From 1991 until 1993 he worked as a theoretical ecologist at the department of Landscape ecology of the Staring Centre (now Alterra) where he studied the dispersal and population dynamics of the badger (*Meles meles*). In 1993 he started a PhD project at the department of Theoretical Production Ecology (WU) comprising modeling and experimental work on the competition, population dynamics and dispersal of grassland species in field boundaries. Since March 1999 he is appointed as a postdoc at the Department of Foodweb Research of the Netherlands Institute of Ecology and the Department of Environmental Science and Water Resources of the IHE-Delft, studying the effect of CO_2 and temperature increase on the competition between aquatic plants.

Publications of the author

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