

**THE ROLE OF PLANT TRAITS
IN THE REGULATION
OF DIVERSITY**

- A MODELLING STUDY -

**DE ROL VAN PLANTENEIGENSCHAPPEN IN DE REGULATIE VAN DIVERSTEIT
- EEN MODELSTUDIE -**

(met een samenvatting in het Nederlands)

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The role of plant traits in the regulation of diversity

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VOOR MIJN OUDERS

“The fact that organisms living in different places are different is easy to explain by Wallacian forces. The question of how so many sorts of organisms are able to persist together in the same ‘place’ is much more difficult to answer, is much more interesting; it demands a biotic interpretation and a Darwinian solution.”

Harper (1977 : 750)

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GENERAL INTRODUCTION

Processes accounting for the maintenance of diversity

The issue of species diversity is an intriguing topic. Since long it has become a central question in community ecology how large numbers of competing species can coexist. Gause (1934) first formulated the classic theory on the relation between competition and diversity. This theory was based on a model made by Lotka (1925) and Volterra (1928). This model was the basis for many later models on competition. Lotka (1925) and Volterra (1928) showed that, when two species competed for similar resources in a similar way, one would always be the superior competitor and eventually outcompete the weaker species. The theory was supported by observations in experimental settings. Later this was called the ‘competitive exclusion principle’ (Hardin, 1960). Considering that plants in a community can partition the available resources, the theory was generalised by stating that the number of species in a community could not exceed the number of limiting resources (e.g. McArthur & Levins, 1964).

Plants in general need the same resources, the most important being light, water and nitrogen. If these are the only important limiting factors, it seems to contrast with the large diversity observed in many natural systems, such as tropical rain forests or chalk grasslands. Since the formulation of Gause’s competitive exclusion principle, theories have been developed that try to solve the paradox of diversity. Palmer (1994) distinguished no less than 120 published theories. These theories can roughly be categorised by their focus on mechanisms that avoid, delay or disrupt competitive exclusion (Palmer, 1994).

Avoid competitive exclusion

When a species in a community increases in abundance it can lead to the extinction of other species in the community. However, it does not always come to that. In some cases, the process can be put to a halt by stabilising mechanisms such as negative density or frequency dependence. For instance, high densities of a species can be more susceptible to species-specific pests. This will prevent the species from being very abundant. Also, as frequency increases, intra-specific competition can reduce a species’ vigour. Accordingly, Lotka -Volterra models predict that species can coexist if intra-specific competition is larger than inter-specific competition.

These kind of self-limitations can also occur less deterministic. A recently emerging theory is that of ‘competitive chaos’ (Huisman & Weissing, 2001; Roelke et al., 2003). Little changes in initial conditions can put a system onto a completely different trajectory of development, and the development in itself can be chaotic. Predicting the outcome of competition in these systems can be extremely difficult, or even impossible.

Another explanation for observed small-scale diversity is the theory of niche differentiation. In 1975, Diamond formally formulated the niche differentiation hypothesis. This states that species will -in order to avoid competition- specialise (or be forced) on a specific combination of resources. As a consequence, the number of available niches will be the upper limit of the number of species in a community. There are many interpretations on the nature of these 'niches'. Niches can represent different resource requirements or different a-biotic conditions in the microhabitat (Leibold, 1995), both available as temporal or spatial 'windows of opportunity' for species to specialise on. Related to this theorem is the resource ratio hypothesis (Tilman, 1985) that supposes that species need specific quantities and combinations of resources. The change in relative availabilities of limiting resources through time or space will result in diversity of species.

A recent theory on the regulation of diversity is the promoting role of diversity on itself: 'Diversity begets diversity'. It argues that diversity gives rise to many different conditions in space and time, providing niches for additional species (Palmer & Maurer, 1997; Franzen, 2001). In this case the question is not why there are so many species coexisting, but rather why there are not more species coexisting.

Variation in life-history theory can also account for coexistence. Competition-colonisation models explain coexistence of species that show a trade-off in competitive ability versus dispersal. The theory states that the most competitive species is a poor disperser and is thus unable to occupy all sites, and the species that is the least competitive is the most likely to reach an empty site. Many species differing in competitive ability were found to be able to coexist as predicted by this theorem. Tilman (1994) even showed that an unlimited amount of species could coexist. Continuous creation of empty patches by disturbance or mortality and consequent establishment of plants herein is the key process for attaining diversity along the rules of this theorem. Other trade-offs, such as seed size and number (Turnbull et al., 1999), competitive ability and mortality (Adler, 1999), or a shift in competitive interactions during life history-stages (Goldberg et al., 2001), can in theory lead to coexistence of plants.

Delay competitive exclusion

A contrasting explanation for the coexistence of species is the suggestion that differences between species are in fact negligible. The more similar species are, the less they will differ in fitness and the longer it will take for the exclusion of one species by the other. Random and neutral processes will dictate the composition of plant communities rather than differences between species. The theory of island biogeography (McArthur & Wilson, 1967) is based on this assumption. In this theory it is argued that species essentially are equivalent in competitive ability, lifespan and reproduction. Site occupation is random. The model was later extended by Hubbel (2001). The theory also bears resemblance to the species-pool model (Eriksson, 1993). In this model the composition is determined by the regional species pool and inter-specific interactions play minor roles. Also the carousel model (van der Maarel & Sykes, 1993) is related. It is stated in this theory that all plants in a similar habitat, for example a grassland, have the

same habitat niche and all plants can find some window of opportunity to establish or re-establish in the community by local plant mortality and high species mobility.

Spatial pattern has also proven a factor in delaying competitive exclusion. As a result of a short dispersal distance, species tend to form mono-specific aggregates. On average, the inter-specific interactions are reduced. This will be advantageous for weaker competitors because on average the competitive pressure of stronger species is less within these aggregates. On the other hand, for strong competitors the competition is more intense because they experience more con-specific interactions. As a consequence the competitive displacement of weak species is delayed (Pacala & Levin, 1997; Chave & Levin, 2002).

Disrupt competitive exclusion

In the absence of disturbance, ecosystems tend to show a succession towards vegetation dominated by a few species. Local disturbance has been regarded as one of the driving factors behind the maintenance of diversity. Disturbance removes part of the vegetation. In those disturbed patches other conditions prevail, for instance caused by relieve of competitive pressure. Species that would be outcompeted at undisturbed patches can establish and grow. Later these disturbed patches again become filled with more competitive species. Local disturbance can thus create a mosaic of different successional stages in communities (Sousa, 1984). At a larger scale, species from different successional stages together will score a high species diversity. This view of plant communities consisting of mosaics of patches is present in a whole range of different theories (see Wu & Levin, 1994).

Under some kind of disturbance, like mowing or grazing, the dominant species will suffer most. This can be because the dominant species are affected disproportionately, for instance because of a tall stature or high palatability. Subordinate species can perform relatively well under such circumstances. By grazing or mowing regimes, several species can exist alongside (Bobbink & Willems, 1993).

A need for mechanisms

All above theories attempt to explain observed patterns of diversity in communities. So far it has been common practice to simplify a system to such an extent that it can hardly be explained exactly why observed patterns occur. Agnew et al. stated in 1993: “ We have not reached the state where we can understand vegetation dynamics by describing mechanisms. In many cases we can at best describe and quantify processes, which later have to be understood by finding underlying mechanisms.” Especially competition has the potential to strongly influence the community structure (Grace & Tilman, 1990; Goldberg & Barton, 1992). The lack of insight in the mechanisms behind competition has hampered progress in the understanding of plant competition (Schwinning & Weiner, 1998; Berntson & Wayne, 2000). Increasing this understanding will aid to build a coherent

theory on plant competition and its role in dynamics, structure and evolution of plant communities (Connolly et al., 2001).

In the competition for light, plants interact by modifying the available light. Within the vegetation, the different leaf layers in the canopy intercept light, creating a vertical light climate. It will depend on the developing light gradient and the position of the plant herein, how it will perform. Plant height and leaf area are the most important traits determining the strength of the interactions between plants, as they determine the amount of light intercepted by a plant itself, as well as affect the quality and quantity of light that is available for neighbouring plants. Height and leaf area traits are the result of characteristics of allocation and growth. Consequently, when studying interactions between plants in a canopy, the investment pattern should be explicitly included. Plants can (or be forced to-) alter their height and leaf area growth in response to the presence of neighbours (Weiner & Thomas, 1992). Competition thus triggers the plant to alter its leaf area and height growth and this affects their competitive interactions. Traits associated with leaf area are, amongst others, specific leaf area, leaf angle, leaf turnover, individual leaf size, leaf nitrogen content, and evaporation of water. Traits associated with height growth are, for instance, stem diameter and the distribution and density of supportive tissue. Changes in these traits can reflect on the root system as well. For plants with a limited lifespan it is not enough to simply withstand competition. During a lifetime, investments have to be made in reproduction to ensure future generations. Species can differ in their timing, extent and duration of investments in reproduction. As one investment goes at the disadvantage of the other, plants have to find the combination of different traits that ensures their perseverance in the vegetation over the years. With so many interacting traits, which also interact with the environment, it is very difficult to distinguish between the influences of different traits on plant performance.

Mechanistic models can be of great help to assess the role of traits in competition. A model system allows singling out the effect of a specific trait separate from other traits or environmental variation. A mechanistic approach is essential for the understanding of observed patterns of plant behaviour. We could simply describe processes involved at each separate scale and use the empirical model for the simulation of plant or population growth. This practice however gives no explanation as to how or why the variables act to affect growth (Tilman, 1990; Weiner, 1995b; Jarvis, 1995).

As competition determines the exclusion of types according to the competitive exclusion principle, this will give insight in the development of the diversity of communities. We developed a model to investigate competitive interactions between plants that possess a variety of traits. We included mechanisms at the plant and organ scale in the simulations of processes at population or community scale. In this way we achieved self-assembling communities without inserting community-level specifications (Colisanti et al., 2001). The community structure we obtained is truly a result of underlying mechanisms. In this thesis, we will try to formulate general statements on the influence of investment patterns on competition, population development and coexistence, independent of variation in external factors for growth.

The model system

The multitude of traits in plants and their intricate behaviour makes them especially interesting to study. However, it makes them difficult to study as well. As already stated, model studies provide a way to disentangle the specific roles that traits play in determining plant behaviour. In this thesis, a closer look is taken on the role of investment in height growth, crown architecture, seed production and dispersal in determining growth, competition and coexistence between plants.

It is important to look at mechanisms at least one scale below the process of interest. Usually, scientists choose one specific scale on which they put their focus. For this scale, only the average of variables is taken into account, not the variation within, for this variation would find its origin in a lower scale. The higher scale variables are taken homogeneous (Rietkerk et. al., 2002). However, by pre-setting the scale of interest, important aspects of the system as a whole can easily be overlooked because results are not emerging from underlying mechanisms. Therefore we focus on the influence of mechanisms at lower scales on higher scale processes. We start by formulating investment strategies, evaluate implications thereof for competition and subsequently evaluate the effect of competition on population development and community development.

When building a model system, simplifications have to be introduced. If too little simplifications are made, the tractability and interpretation of model results will be difficult. It is possible that with many parameters, the model will become overly sensitive to changes in the input values because many parameters may interact. Also, a lot of data will have to be gathered for parameterisation. On the other hand, using a lot of restricting assumptions can make the model inflexible (Snowling & Kramer, 2001). While sufficient detail should be built into a model, it should not become too complex. A solution is to only include those traits that are important to gain understanding of a particular process. When modelling the effect of plant shape in an environment where light is the single limiting factor, light-harvesting traits like height and leaf area growth will obviously have to be incorporated in the basic model. Other factors, for instance nitrogen, also play a crucial role in plant growth. But, because in our case the focus is not on below ground processes or plant physiology, introducing nitrogen as a factor will only confound the effects of traits directly related to light. Hence, in the case of nitrogen, its availability should be set constant. Eventually, when a simple basic model is constructed, other factors affecting plant growth should preferably be introduced one at the time. No new factor should be introduced until the effect of an earlier included factor is clear. The evaluated factor can consequently be removed, or set to a constant. In this way we are building up an understanding of the intertwining effects of different sets of traits. In this thesis we show that with a simple basic model and a few varying factors per simulation, an ecologically meaningful, comprehensible and interpretable result will follow.

As a consequence of this approach, the model plants described in this thesis lack quite a number of functional traits. Plants in a real-life situation have more complex characteristics and strategies, involving many traits that can have differential effects on the performance and fitness. In addition, these real-life plants are subject to much more

diverse influences from the environment. The final phenotype of a real-life plant is a compromise between a myriad of selection pressures (Roff, 1981). The purpose of a theoretical study such as this one is therefore not to make accurate predictions on the performance of any particular real-life plant. Rather, it is intended as a generator of new insights and ideas about the role of particular traits in the patterns of performance of plants growing in isolation or competition. We think that the ‘bottom up’ approach from a combination of a more mechanistic basis for the simulation of larger scale processes has the potential for revealing much about the how and why of many of these processes. So far studies with such an approach are few.

Optimisation in an evolutionary context

We discussed the need for a mechanistic basis to understand the origin of higher-level processes such as population growth and community diversity. To evaluate the performance of a species, a measure of fitness has to be assigned. To maintain a simple system, we focus our investigations on plants with a single growing season. Because we are interested in the performance on longer time-scales, a fitness measure that has value only over a single growing season (like biomass) is not sufficient. One way for a plant to maintain itself in a community is to divert resources to produce offspring. We assume that, the higher the lifetime production of offspring, the higher the fitness.

It is logical to assume that a species that produces more offspring in its lifetime than other species increases faster in abundance. Therefore, a species adopting a new trait that enhances its fitness, or changes the value of a trait to increase fitness, will readily become abundant in a community. Individuals lacking the trait will get relatively less abundant. Optimisation theory seeks to find those (values of-) traits that give the plant maximum fitness (Levin & Muller Landau, 2000). The fitness will depend on the environment and the restrictions that the plant meets in architecture or trade-offs. For a given environment it can be calculated or simulated which (value of a-) trait results in the highest fitness. This will give a prediction of or an explanation for which value of a trait will be most widespread in a community. Research has for example been done on optimal root-shoot ratios (Hilbert, 1990; Reynolds & Chen, 1996) timing of reproduction (Cohen, 1971; Iwasa, 2000) leaf nitrogen distribution (Hirose & Werger, 1987) and many other things.

Optimisation theory however always assumes that the environment is completely predictable for the plant. It is of course unrealistic to assume that plants can ‘foresee’ the environmental conditions over a growing season (Reynolds & Chen, 1996). The light climate, for instance, is influenced not only by the growth of the plant itself but also by the architecture and growth traits of competitors. If conditions change, the value of the optimal response will change. In a competitive environment, the question which trait value is optimal in response to the environment is not valid. A more appropriate question is what value of a trait is optimal in response to plants with other traits that interfere with conditions constantly.

Taking the reasoning a level higher, we can state that fitness is also not static over the course of years. Fitness will depend on the changing frequency and abundance of competitors, which themselves are subject to the changing conditions. Additionally, it might not even be necessary for a plant to respond optimally. If the response is such that it is fitter than the competitors, it will perform better. Calculations on the performance of individuals or groups of plants possessing a particular trait value in this kind of competitive setting are generally referred to as game theory. Game theoretic methods are a powerful way of assessing the fitness of individuals in an environment consisting of many different species (Levin & Muller Landau, 2000). It is thus suitable to address the question of maintenance of diversity. In Chapter 4 and 5 (and less explicitly, Chapter 6) of this thesis we make use of game theory to assess the performance of plants possessing certain traits. Therefore we give a short overview of the development and theory, explaining terms that will be used further on in this thesis.

Game theory as a tool

An early application of game theory to biology is by Maynard Smith & Price (1973). His game consists of two types of players, Hawk and Dove, which compete for a resource. In this game, each player gets some specified proportion of the resource, depending on the opponent they encounter. The proportion of resource that is acquired in the encounter is the ‘pay-off’ of the encounter. The pay-off is assigned per game of competing Hawk-Hawk, Hawk-Dove or Dove-Dove. It depends on the strategy adopted by the opponent which strategy can best be adopted by the player.

Traditionally in game theory, a value or measure of success is assigned to the benefits received from playing a particular strategy. The pay-off of a player is assigned with a function, to cover all potential situations (Vincent & Cressman, 2000) or assigned per game like Maynard Smith and Price did (Riechert & Hammerstein, 1983). Because in the competition for light the dynamics of interacting plants are asymmetric and thus non-linear, it is nearly impossible to catch the behaviour of the system in one single pay-off function or a simple value. A possibility to overcome this limitation is to numerically calculate the pay-off of plants playing a game instead of assigning a simple function or value. This way the mechanisms that determine the behaviour of the system with its complex a-symmetric connections can be included. We thus link the dynamics of light competition to game-dynamic calculations.

Lewontin (1961) first explicitly introduced frequency dynamics for game theory, giving rise to evolutionary game theory. In evolutionary game theory, as opposed to classic game theory, players have fixed strategies rather than being able to choose (a set of-) strategies. The success of a strategy is defined in terms of the number of copies that a strategy will leave of itself to play in the games of succeeding generations. The strategies themselves are therefore the players, and the games they play are dynamic rather than static (Ross, 2003).

With evolutionary game theory, the time course and outcome of competitive interactions can be determined over more than one generation. Players with a large pay-

off relative to the other players will increase in number. Consequently, the frequency at which they occur in the community will increase. This change in the composition of the community will alter the influence of the community as a whole on the pay-off of a single player. If eventually the community comes into equilibrium, there is no change in the frequencies of the players involved. One possibility is that there is a monomorphic equilibrium. In this case only one strategy is left. Another possibility is that there are more strategies that have an equal fitness at equilibrium. This would mean that the equilibrium is polymorphic. Another possibility is that there are alternating winning strategies and the system never reaches equilibrium. This can occur when the winning strategy depends highly on the composition of the community and this composition continuously changes during successive calculations. The strategy (or strategies) that has maximised fitness given the opponents is the Nash solution. A strategy that is present at Nash equilibrium is an evolutionary stable strategy (ESS) if no individual can improve its fitness by changing the value of its trait and thus no mutant strategy can invade the population (Maynard Smith, 1982).

Outline of this thesis

In this thesis, we try to slowly build up an understanding of the role of a limited set of plant traits in the competition between plants, population growth, and finally, the composition of the community. In Chapter 2, we describe a basic mechanistic plant growth model. The driving forces behind plant growth in this model are light availability, plant architecture, photosynthesis and allocation. With this model as a basis, specific growth strategies of plants are explicitly incorporated in later chapters. Subsequently growth and fitness of plants are simulated, for single plants as well as plants in a competitive context.

In Chapter 3, we explore coexistence possibilities for pairs of plant types differing in the investment in height growth. In these types, the investment in height growth trades off with leaf area investment. We investigate whether types with different height investment can gain similar fitness in a competitive context. Furthermore, the role of frequency dependent processes on coexistence between two plant types is studied.

In Chapter 4, we explore the ESS height investment in various environments and for plant types with various traits. The influence of density, season length, plasticity and distribution of leaf area over height on the ESS height investment is investigated. This is done in a game-theoretic framework. At the same time, we investigate the possibilities for coexistence for these various types in the different environmental conditions. Finally we explore the role of explicit space for the coexistence of different height investment types.

In Chapter 5, we investigate the adaptive value for different seed allocation strategies, also in a game-theoretic framework. Plant types differ in their timing of a switch from vegetative to seed production. There is thus a clear trade-off in fecundity and competitive strength. Also, the effect of reintroduction of extinct types is studied.

In Chapter 6, we investigate the effect of dispersal distance on the competitiveness of plant types. The types differ in competitive strength as a result of a

trade-off between vegetative growth and seed production. Types disperse and grow in a spatially explicit area. We explore the influence of dispersal distance on population development of types of equal strength and different strength. Also, the effect of clustering on the population development is studied. Finally, we check if coexistence by means of a competition/colonisation trade-off is possible for these types, without additional disturbances.

In Chapter 7, we study the effect of the vertical distribution of leaf area on the performance of the plant, in isolation or competition. Plants in this chapter can bring their leaf area to higher positions along their stem (e.g. change their crown shape) under the influence of shade. Plants can differ in the rate with which they can change the shape of their crown, and the extent. In contrast with the former chapters, plants grow according to a pipe theory model. Stem volume is not determined by an allometric function, but by the leaf area and its distribution along the height of the plant.

In Chapter 8 we discuss and summarize the results that were obtained in the previous chapters. We also discuss the possible influence of omitted traits and other factors that were not treated in the various chapters, which could promote coexistence.

**A MECHANISTIC MODEL
FOR THE SIMULATION OF GROWTH AND FITNESS
OF ANNUAL PLANTS**

Summary

Although in many models the relation between life-history traits is implicitly assumed to result from alternative allocation of resources, explicit mechanistic models of this allocation process are few. We describe a dynamic mechanistic simulation model, suitable for the simulation of growth of competing annual plants in mixed stands. Most important features of this model are: 1. The specific pattern of allocation per plant. 2. Growth according to a strict carbon balance. 3. The inclusion of crown architecture. The model is based on the process of photosynthesis. Plants compete in a defined space, with complete mixing of leaves. Height, leaf area and leaf distribution parameters specify the shape of the plant. The fitness of individuals is measured as the amount of carbon investment in seed at the end of a defined growing period. Model assumptions include plastic allocation patterns as a response to the local light climate, which is influenced by the characteristics of the plant itself and neighbouring plants. The model will allow for the evaluation of the fitness value of separate traits in the competition for light, ontogenetic investment patterns and plasticity. In addition, it can be used for evaluation of the fitness of trait combinations.

Keywords: crown architecture, carbon balance, allocation pattern, mechanistic model, dynamic, plant growth

Introduction

Competition for light can be a major factor in determining species performance in dense stands. It is quite obvious that in the direct competition for light, the light capturing ability of plants will be of the utmost importance. Plant architecture will be one of the most important features that determine light capturing ability of a plant (Skalova et al., 1999). Numerous studies have tried to assess the role of different plant architecture characteristics for light acquisition under competitive circumstances (e.g. Mitchley, 1988; Teughels et al., 1995; Hirose & Werger, 1995; Schwinning & Weiner, 1998; Aerts, 1999; Anten & Hirose, 1999; Werger et al., 2002). These studies agree that light-capturing ability of individuals is determined in particular by two characteristics. Firstly, leaf area determines the surface with which the plant can capture light. Secondly, positions of the leaves in the vertical light gradient determine what light intensity leaves experience. This is specified by the height of the plant and the vertical distribution of leaf area over the height.

To improve light capture in a crowded vegetation, species might allocate more of their currently acquired carbohydrates to either height or leaf area growth. A species may be plastic or rigid in this allocation. Many studies show that plants alter their allocation pattern as a response to the environment they experience, in order to reduce or avoid competitive suppression (Schmitt, 1997; Schwinning & Weiner, 1998; Dorn et al., 2000; Weinig, 2000). As species allocate their biomass and grow, the available light in the vegetation changes. This change affects not only the total light availability but also the light available in the different layers of the vegetation. The adequacy of allocation strategies to improve light capture may vary under this vertical and temporal variation of the light climate. Thus, besides leaf area and the position of the leaf area over the height of the stand, the lifetime pattern of allocation to light harvesting characteristics is an important feature of overall plant competitive ability.

To gain insight on the limits and possibilities of shape and allocation strategies of plants, a modelling approach is suitable. Models can represent a well-defined system in which questions can strategically be tested. Is the set of plant shape characteristics and plastic responses beneficial for the given species? What is the range of circumstances in which a certain strategy is most effective? The questions become more complex when spatial and temporal dynamics are taken into account. For gaining insight in the above questions, a descriptive model is insufficient. We focus on explanatory models because a non-deterministic nature of links between plant architectural traits, cost and benefits is essential to achieve an understanding of how and why processes and traits interact (Tilman, 1990). For this purpose, processes on at least one hierarchical level deeper than the response described should be included (Jarvis, 1995). Three elements are important for a concise simulation of mechanistic plant growth under light limiting conditions. The first important aspect is an explicit architecture. This will determine the exact light interception of plants in relation to neighbouring plants. Secondly, an explicit lifetime allocation pattern to different plant functions is needed. Thirdly, these two characteristics should be linked through a carbon balance. The carbon balance includes elements such as

photosynthesis, growth and maintenance. Explicit calculations of resource capture and costs for growth and maintenance enable us to make sound comparisons between the performances of plants with different allocation strategies.

For the simulation of plant growth and light interception, a myriad of models is available. A large part of these models is descriptive or partly descriptive. Especially leaf area is often modelled as a function of plant developmental stage or simply as an input parameter (Marcelis et al., 1998). Relatively few models have an explicit leaf area distribution for plants (but see Lieth & Reynolds, 1988) and at the same time have been applied to simulate light interception and photosynthesis in a mixed stand (but see Tournebize & Sinoquet, 1995; Anten & Hirose, 1999; 2003). Even rarer is the appliance of such models in a dynamical setting, which is necessary for understanding and assessing the importance of different structures over the life-time performance of a plant (but see Yokozawa & Hara, 1992; Yokozawa et al., 1996; Caton et al., 1999; Sekimura et al., 2000, Schippers & Kropff, 2001). Models do not usually combine all elements.

In the model developed in this chapter, individuals grow mechanistically according to a carbon balance. The plant growth is mechanistic in the way that growth of plant organs is not superimposed on the plant, but is determined by the allocation to those organs and the costs and benefits this incurs. In the model, it is possible to assign a species-specific allocation pattern to each individual. Plasticity in height growth is implemented as a response to shading. The extent to which a plant is plastic can be adjusted. Plants in this chapter have an explicit vertical distribution of leaves, so the quantity of photons intercepted over the vertical light gradient relative to other individuals can be calculated. The model can be used to assess the role of specific traits in the competition for light (Chapter 3 and 7). Also, it can be extended towards population dynamics (Chapter 4, 5 and 6) and can be made spatially explicit (Chapter 6).

In the following sections in this chapter, the basic features of the model are described. In Section 1, the shape of the aboveground part is discussed. The calculation of the light climate is dealt with in Section 2. In Section 3, leaf and plant photosynthesis is specified. The carbon balance is described explicitly in Section 4. In Section 5 the allocation program of the plant is explained.

1. Shape of the Model plant

A plant is confined to grow in a predetermined surface area, referred to as a cell. More than one plant can inhabit this cell. Horizontally, the plants in a single cell are perfectly mixed. Obviously, in real vegetations, plants do not completely overlap each other. In the approach taken here, an overestimation is made on the extent of plant interaction. However, by taking the cell as unit in which plants grow, and thus standardising the leaf area overlap, we can make easy comparisons between cells. This eliminates the variation in competitive pressure on individuals that would otherwise be caused by different levels of overlap between plants. For that reason, it is a more insightful way of interference analysis.

Each plant has a specified smooth distribution of infinitesimal small leaf elements over its height. The description of leaf area distribution in a single formula allows for a straight forward calculation of the rate of change in the shape of the curve. The leaf area distribution in leaf area per unit height per cell basal area is described by the following formula (Caton et al., 1999):

$$\text{Leaf area distribution} \quad \lambda(h) = p_0 \cdot \frac{L_t}{h_{pt}} \cdot \left(\frac{h}{h_{pt}} \right)^{p_1} \cdot \left(1 - \frac{h}{h_{pt}} \right)^{p_2} \quad (1.1)$$

in which h_p is the height of the plant at time t , L is leaf area index at time t , h is the height at which the leaf density is calculated and p_0 , p_1 , p_2 are shape parameters. By dividing the leaf area by the height of the plant, the leaf area distribution is made independent of plant height. I.e., by taking h/h_{pt} as x , one can write for the total leaf area L_t

$$\text{Total leaf area} \quad L_t = \int_0^{h_{pt}} dh \cdot \lambda(h) = L_t \cdot \int_0^1 dx \cdot p_0 \cdot x^{p_1} \cdot (1-x)^{p_2} \quad (1.2)$$

Hence the shape parameter p_0 is given in terms of p_1 and p_2 by the integral

$$\text{Shape parameter} \quad p_0 = \frac{1}{\int_0^1 dx \cdot x^{p_1} \cdot (1-x)^{p_2}} \quad (1.3)$$

By changing the shape parameters p_1 and p_2 different leaf area distribution curves can be achieved. See Figure 3 in Appendix 1 for examples.

The relation between height h_{pt} and stem volume S_t at time t is given by a standard allometric formula (Stearns, 1992):

$$\text{Stem volume} \quad S_t = \alpha \cdot h_{pt}^\beta \quad (1.4)$$

Here α and β are constants.

Although a root system is present in the model plant, it is not functional. It merely acts as a carbon sink for the carbohydrates from photosynthesis. The root weight is a linear function of the leaf area:

$$\text{Root mass} \quad R_t = \sigma \cdot L_t \quad (1.5)$$

2. Light climate

We assume a light climate in the vegetation cell in which the photons flow vertically downward. At each depth h the interception of light by the plants is modelled by Beer's law (Monsi & Saeki, 1953). The light extinction rate at height h is calculated from the leaf area, leaf inclination in the horizontal plane and absorption coefficient of leaves of all plants in the cell:

$$\text{Light extinction rate} \quad d_h i_h = -i_h \cdot \sum_{\text{allplants}} \lambda(h) \cdot \cos \alpha \cdot a \quad (2.1)$$

Here $\cos \alpha$ is the leaf inclination and a is the absorption coefficient of leaves. By integration of 2.1, the horizontal light intensity $i_h(h)$ is given for each height h in the cell:

$$\text{Light climate} \quad i_h(h) = i_h(h_v) \cdot \exp \left[- \int_h^{h_v} \sum_{\text{allplants}} dh \cdot \lambda(h) \cdot \cos \alpha \cdot a \right] \quad (2.2)$$

where $i_h(h_v)$ is the horizontal light intensity above the vegetation and h_v is the height of the vegetation. It is assumed that the cells receive an average light intensity over a season; in other words it does not vary during the development of the plants. This assumption will make model results simpler to interpret. The influence of a seasonally variable light climate will be assessed in Chapter 5.

The rate of photon absorption for the leaf elements at height h is calculated from the light climate at height h , the leaf inclination and absorption coefficient of a plant. It is given by

$$\text{Light interception} \quad i_{al}(h) = i_h(h) \cdot \cos \alpha \cdot a \quad (2.3)$$

During a simulation of the growth of plants in an individual cell, the vertical light climate not necessarily has a smooth distribution over the height of the vegetation. Therefore, at each time step, the light climate is calculated with the fourth order Runge-Kutta method. This integration method evaluates the rate of change at several points in each step and can approximate the vertical light climate in an accurate way (Press et al., 1989).

3. Leaf and plant photosynthetic rates

The leaf photosynthetic rate is calculated on the basis of the non-rectangular hyperbolic relationship between maximum photosynthetic capacity, light interception and quantum yield. This relationship accurately reproduces the curve of photosynthetic capacity in actual plants (Marshall & Biscoe, 1980).

$$\text{Leaf Photosynthetic rate } P_{gl}(h) = P_{ml} \cdot \frac{(1+x) - \sqrt{(1+x)^2 - 4 \cdot \theta \cdot x}}{2 \cdot \theta} \quad (3.1)$$

$$\text{With } x = \frac{\Phi \cdot i_{al}(h)}{P_{ml}}$$

Here P_{ml} is the photosynthetic capacity of the leaves, Φ the quantum yield per unit absorbed light, θ a curvature factor and $i_{al}(h)$ is the rate of photon absorption of the leaves at height h (see 2.4). It should be noted that for reasons of simplicity we assume that capacity P_{ml} , quantum yield Φ and curvature θ do not vary with height.

For each plant the total photosynthetic rate is given by the integral over the plant's height, of the leaf photosynthetic rate times the leaf area. This gross photosynthesis is in μmol carbon per unit time.

$$\text{Plant Gross Photosynthetic rate } P_g = \int_0^{h_p} dh \cdot P_{gl}(h) \cdot \lambda(h) \quad (3.2)$$

Equation 3.2 is calculated using the Gaussian integration method, which is very accurate for smooth functions (Press et al., 1989) such as the leaf distribution formula.

R_m is the maintenance rate, which is based on the carbon weight of the plant parts. It is of the form

$$\text{Maintenance rate } R_m = r_{ml} \cdot L_c + r_{ms} \cdot S_c + r_{mr} \cdot R_c \quad (3.3)$$

in which r_{ml} , r_{ms} , r_{mr} are the maintenance respiration rates in gram carbon per unit carbon mass per unit time and L_c , S_c , R_c are respectively the leaf, stem and root carbon masses at time t . These carbon masses are calculated with help of conversion factors.

$$\text{Leaf carbon mass } L_c = c_l \cdot L \quad (3.4)$$

$$\text{Stem carbon mass } S_c = c_s \cdot S \quad (3.5)$$

$$\text{Root carbon mass } R_c = c_r \cdot R \quad (3.6)$$

Here c_l is in g carbon per m^2 leaf, c_s is in g carbon per volume stem, c_r is in g carbon per gram roots.

In real systems, seeds are cast from the plant at some point in time and are then physiologically independent from the plant. In this model it is assumed that after an initial

investment, seeds no longer are an integral part of the plant. Therefore seed mass is not included in the calculation of the plant's maintenance respiration. The calculation of the allocation rate of carbon to seed is treated in section 4.

4. Growth and the carbon balance

Plant growth is calculated as the growth in stem, leaves and roots. A part of gross photosynthesis is allocated to seed. Seed mass can be seen as a fitness parameter, a measure of how well the individual has performed. The plant allocates carbon to seed only if it is in reproductive mode. A fixed portion of carbon (f_c) from net photosynthesis is then preferentially allocated to seed mass production before the allocation to leaf, stem and root, but after the allocation to maintenance respiration. With the production of seed mass, a certain amount of carbon is respired in growth respiration. The carbon consumption rate for seed mass production F_m is:

$$\text{Carbon consumption for Seed mass} \quad C_{cf} = (c_f + r_f) \cdot d_t F_m \quad (4.1)$$

in which c_f is the carbon per gram seed mass and r_f the growth respiration constant. It should be noted that, if net photosynthesis is negative or zero before allocation to seed, the allocation rate to seed is zero. Once generated, seed mass is assumed to no longer be an integrated part of the plant. Seeds need no additional carbon from net photosynthesis for e.g. maintenance respiration. Therefore seed mass is not taken into account in the carbon balance any further. The net photosynthesis considered in the remainder of this chapter is the net photosynthesis after allocation to seed:

$$\text{Net photosynthesis} \quad P_n = P_g - R_m - (c_f + r_f) \cdot d_t F_m \quad (4.2)$$

At any time t , leaf area L and height h_p together with the constant shape parameter p_1 and p_2 completely determine the shape of the plant. If at any time the leaf area is equal to zero, the plant is considered dead. Growth of the plant in leaf area $d_t L$ and height $d_t h_p$ is related to the consumption and production rate of carbohydrates. Growth is imposed on the plant according to its carbon balance. This means the net carbon consumption rate of the plant has, at any time, to be equal to the rate of net photosynthesis. The net carbon consumption rate results from the carbon costs associated with the production of stem volume and production or removal of leaf area and roots.

Leaf and root elements are shed or produced solely as a result of the carbon balance or a change in shape. Leaf area and root productions require two investments, the carbon invested in mass and the respiratory costs. When leaves or roots are shed, only a part of the previously invested carbon can be retrieved.

If the leaf area growth rate $d_t L$ is positive, the associated carbon consumption rate is

$$\text{Carbon consumption rate for leaves} \quad C_{cl} = (c_l + r_l) \cdot d_t L \quad (4.3)$$

with c_l the carbon content of leaves in gram carbon per unit leaf area and r_l the growth respiration costs in gram carbon per invested gram carbon.

If the leaf area growth rate $d_t L$ is negative, the associated carbon production rate is

$$\text{Carbon production rate for leaves} \quad C_{pl} = c_{rl} \cdot d_t L \quad (4.4)$$

with c_{rl} the retrievable carbon in the leaves in gram carbon per gram of carbon in the leaves. In the case that a plant sheds its leaves, only a part of the carbon is recovered.

The rate of a change in root mass $d_t R$ is a function of the change in leaf area.

$$\text{Root growth rate} \quad d_t R = \sigma \cdot d_t L \quad (4.5)$$

with σ the ratio with which leaf area and root mass change. As can be derived from this formula, we assume a balance between leaf and roots. This means that shedding or growth of leaf elements is coupled with shedding or growth of root elements.

The associated carbon consumption rate for roots if $d_t L > 0$ is

$$\text{Carbon consumption rate for roots} \quad C_{cr} = (c_r + r_r) \cdot \sigma \cdot d_t L \quad (4.6)$$

with r_r the growth respiration costs in gram carbon per invested unit root carbon.

If $d_t L < 0$ then

$$\text{Carbon production rate for roots} \quad C_{pr} = c_{rr} \cdot \sigma \cdot d_t L \quad (4.7)$$

with c_{rr} the retrievable carbon in the roots in gram carbon per gram carbon in the roots. As is the case with leaf area, only a part of the carbon invested in root mass can be recovered.

If a plant grows in height h_p with rate $d_t h_p$ this requires an investment of carbon. This carbon investment consists of two parts. First, for the carbon consumption rate associated with the growth in stem volume (which is equivalent to mass) we can write

$$\text{C consumption rate} \quad C_{ch} = (r_s + c_s) \cdot d_t S = (r_s + c_s) \cdot d_{h_p} S \cdot d_t h_p \quad (4.8)$$

Second, if a plant changes in shape by either height growth or changing the shape parameters p_1 and p_2 , leaf area has both to be produced and shed at a corresponding rate in order to maintain the shape of the plant (see Figure 1). To find the region over which the leaf area change with height $d_{hp} \lambda$ is positive or negative, we determine the value of h^* at which the leaf area change rate is zero. For the calculation of h^* , see Appendix 2.

Point of no leaf area change
$$h^* = \frac{1 + p_1}{1 + p_1 + p_2} \cdot d_t h_p \quad (4.9)$$

As can be seen in Figure 1, $d_{hp} \lambda$ is positive above h^* and negative below h^* (provided that $d_t h_p > 0$). The positive part of the function can be integrated to assess the total leaf area production rate with height growth. The negative part of the function can be integrated to assess the total rate of leaf area shedding with height growth. The integration is done with help of the Gaussian integration method.

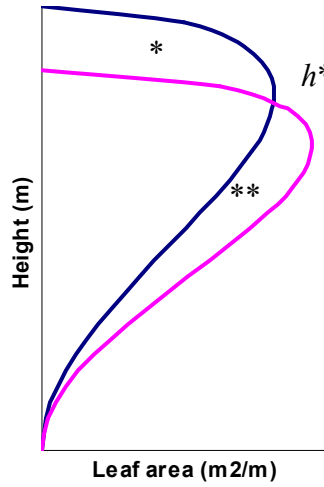


Figure 1. The change in plant shape with height growth. Leaf area has to be redistributed in order to maintain the shape of the plant, as imposed on the plant by Formula 1.2. The area indicated by * depicts the leaf area that has to be newly produced. The area indicated by ** is the leaf area that has to be cast away. The point at which the leaf area change is zero is depicted by h^* .

In formal terms, if a plant grows in height with a certain rate $d_t h_p$, the rate at which leaf area L_r is shed by the plant is calculated by integrating the negative rate of change. This is given by

$$\text{Leaf area shed} \quad d_t L_r = \int_0^{h_p} dh \cdot NEG(d_{h_p} \lambda) \cdot d_t h_p \quad (4.10)$$

The rate at which leaf area L_p is then produced by the plant is calculated by integrating the positive rate of change. This is given by

$$\text{Leaf area produced} \quad d_t L_p = \int_0^{h_p} dh \cdot POS(d_{h_p} \lambda) \cdot d_t h_p \quad (4.11)$$

Hence the value for the NEG part of the function is zero if the value is positive, and $d_{h_p} \lambda$ if negative. For POS, this is the other way around. In the case of mere reallocation of leaves (e.g. no change in total leaf area) the leaf area that is produced is per definition always equal to the leaf area that is shed, e.g. $d_t L_r = d_t L_p$. Because the cost for producing leaves is larger than the carbon that can be retrieved, the plant will have to pay for the reallocation of the leaves. The total carbon consumption rate associated with the leaf reallocation is

$$\text{Leaf reallocation costs} \quad C_{c\lambda} = (c_l + r_l) \cdot d_t L_p - c_{rl} \cdot d_t L_r \quad (4.12)$$

It should be noted that rearrangement of leaf area does not involve any change in the roots. The leaf rearrangement is due to changes in the above ground plant shape and it is assumed to have no consequences underground.

To summarise the processes involved in the carbon balance: The consumption of carbon should at any time be equal to the carbon gain from net photosynthesis P_n . Height growth rate $d_t h_p$ is always non-negative. Leaf area rate $d_t L$ can be either positive or negative, depending on the carbon balance after height growth and reallocation of leaves. If root mass and leaf area are zero, the plant is considered dead.

The production rate of seed mass $d_t F_m$ is not considered in the carbon balance. It is assumed that, if the plant is in reproductive mode, the seed production occurs before growth of any other plant structure.

In case of a positive leaf production rate ($d_t L > 0$) we write

$$P_n = (c_l + r_l) \cdot d_t L + c_s \cdot d_{h_p} S \cdot d_t h_p + (c_r + r_r) \cdot \sigma \cdot d_t L + \left[(c_l + r_l) \int_0^{h_p} dh \cdot POS(d_{h_p} \lambda) - c_{rl} \int_0^{h_p} dh \cdot NEG(d_{h_p} \lambda) \right] \cdot d_t h_p \quad (4.13)$$

Rewriting this gives

$$P_n = [(c_l + r_l) + \sigma(c_r + r_r)] \cdot d_t L + \left[c_s \cdot d_{h_p} S + (c_l + r_l) \int_0^{h_p} dh \cdot POS(d_{h_p} \lambda) - c_{rl} \int_0^{h_p} dh \cdot NEG(d_{h_p} \lambda) \right] \cdot d_t h_p \quad (4.14)$$

In case of a negative leaf production rate ($d_t L < 0$) we write

$$P_n = -c_{rl} \cdot d_t L + c_s \cdot d_{h_p} S \cdot d_t h_p + (-c_{rr} \cdot \sigma \cdot d_t L) + \left[(c_l + r_l) \int_0^{h_p} dh \cdot POS(d_{h_p} \lambda) - c_{rl} \int_0^{h_p} dh \cdot NEG(d_{h_p} \lambda) \right] \cdot d_t h_p \quad (4.15)$$

Rewriting this gives

$$P_n = [-(c_{rl} + \sigma \cdot c_{rr})] \cdot d_t L + \left[c_s \cdot d_{h_p} S + (c_l + r_l) \int_0^{h_p} dh \cdot POS(d_{h_p} \lambda) - c_{rl} \int_0^{h_p} dh \cdot NEG(d_{h_p} \lambda) \right] \cdot d_t h_p \quad (4.16)$$

From the equations 4.14 and 4.16 it is clear that the sign of $d_t L$ is determined by the magnitudes of the term $f_{hp}(L, h_p) d_t h_p$ and the magnitude of the net photosynthetic rate. That is, we can write (as derived from 4.14 or 4.16):

$$\text{Leaf area change} \quad f_L(L, h_p) d_t L = f_{h_p}(L, h_p) \cdot d_t h_p + P_n \quad (4.17)$$

This means that to find the explicit expression for $d_t L$ we must look at the expression for height growth rate $d_t h_p$. In the following section we will formulate how the plant 'steers' its growth rate in height.

5. The allocation program of the plant

Investments in plant organs are made in a hierarchical manner. Firstly, the plant allocates carbons to account for maintenance costs in our model. For annuals it is important to produce seeds, for the plant does not survive until the next growing season. It can be assumed that for annual plants, at some point the allocation to reproduction will be preferred over other structures. Therefore, if the plant is in reproductive mode, the second priority is allocation to seed. After maintenance and seed investment, plants allocate

biomass to different organs like leaves, root or stem. Because of the asymmetrical nature of the competition for light, height will be important for a plant's competitive status. The priority of mass investment lies therefore with stem investment. Finally, the plant invests whatever is left from net photosynthesis in leaf area and roots. In Figure 2 the order of carbon allocation to various organs is depicted.

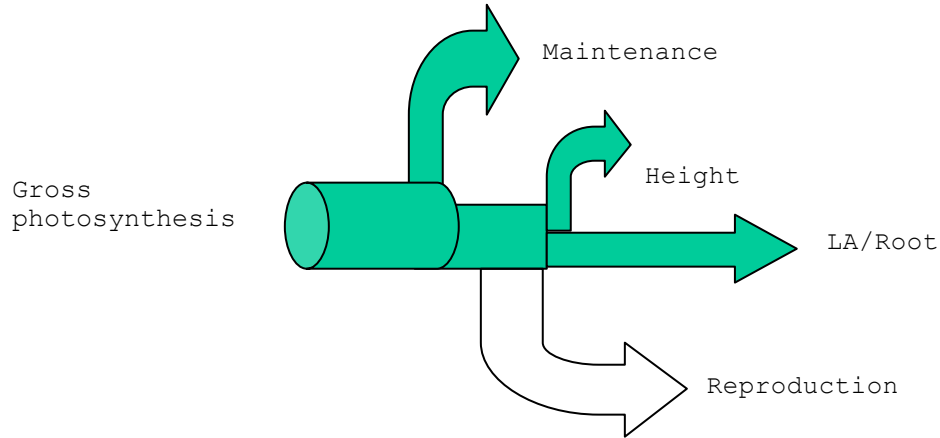


Figure 2. The allocation hierarchy of the model plants. From the pool of gross photosynthesis, carbon is allocated to: 1) Maintenance 2) Reproduction, if the plant is in reproductive mode 3) Height 4) Leaf area and roots.

The allocation pattern can be static, or change over time depending on ontogenetic development or environmental conditions. In the latter case, the response of a plant is plastic. A well-known plastic response in plants is the 'shade avoidance' response, which is triggered by an altered red /far-red ratio and is mediated by the phytochrome (Cipollini & Schultz, 1999). Inside a vegetation canopy, the spectral composition of light is altered by absorption of light in the red region of the spectrum. By this process, the red/far red ratio changes. These changes are reliably correlated with the presence of neighbours (Schmitt, 1997) and it is well known that plants can detect these changes in red/far red ratio. Plants will often show an increased allocation to the stem part when grown under such an altered red/far red regime (Schmitt et al., 1999). The plant is thus able to grow taller and has a chance of reaching a better light climate. In this way, plasticity allows to avoid possible costs from shading by competitors (Dorn et al., 2000; Weinig, 2000a). The ratio of red to far-red wavelengths is an accurate signal of vegetation shade (Smith, 1982). It is therefore assumed in this model that the red/far red 'signal' for an individual plant scales directly with the amount of light that this plant is deprived from by surrounding leaves. This includes the plant's own leaves.

The extent of the height growth rate $d_t h_p$ for the plants in this model is dependent on three factors: the plasticity of the plant to grow in height, the severity of shading and the net photosynthesis. The plasticity in allocation can be considered as the inherent tendency to react on shading (e.g. reaction norm, de Jong, 1995). This will be species-dependent.

$$\text{Height growth rate} \quad d_t h_p = f(a_s, S_{\text{signal}}, P_n) \quad (5.1)$$

in which a_s is the maximum allocation to height growth, S_{signal} the shading signal and P_n the net photosynthesis.

Relative light interception is used as a measure S_{signal} of shading. The actual intercepted light of the plant is compared to the possible intercepted light when no light is lost as a result of shading.

$$\text{Actual intercepted light} \quad I_h = \int_0^{h_p} dh \cdot \lambda(h) \cdot i_{al}(h) \quad (5.2)$$

$$\text{Possible intercepted light} \quad I_{hr} = \int_0^{h_p} dh \cdot \lambda(h) \cdot i_{al}(h_p) = i_{al}(h_p) \cdot L \quad (5.3)$$

In these formula's I_h is the total of actual intercepted light, and I_{hr} is the possible intercepted light if there would be no shading. The actual intercepted light relative to the possible intercepted light in absence of a light climate is:

$$\text{Relative intercepted light} \quad \frac{I_h}{I_{hr}} = \frac{1}{L} \cdot \int_0^{h_p} dh \cdot \lambda(h) \cdot \frac{i_{al}(h)}{i_{al}(h_p)} \quad (5.4)$$

From this equation we calculate the shading signal.

$$\text{Red/far-red signal} \quad S_{\text{signal}} = 1 - \frac{I_h}{I_{hr}} \quad (5.5)$$

As explained before, no distinction is made between shading by neighbours and self-shading. From the equation for the signal S_{signal} can be derived that, under conditions of complete shading, the value of the shading signal is one. In this case the maximal investment in height $P_n \cdot a_s$ will be done. It can also be derived that the value of the signal approaches zero if there is no shading on any of the leaves. All available carbon from net photosynthesis is consequently allocated to leaf and root growth and none to height growth. It is also possible to adjust the functional response of the plant to shading. If a

functional response is introduced, S_{signal} has to be replaced with FR_{signal} in the formulas for height growth.

$$\text{Functional response to shading} \quad FR_{\text{signal}} = \frac{c \cdot S_{\text{signal}}}{1 + d * S_{\text{signal}}} \quad (5.6)$$

In this formula c and d are constant parameters.

The height growth $d_t h_p$ is calculated from the relation between stem volume and height, the carbon allocated to height growth as determined from net photosynthesis P_n , maximum allocation of carbon to height growth a_s and the shading signal S_{signal} . This can be written as

$$\text{Height growth rate} \quad d_t h_p = d_t \cdot \frac{(P_n \cdot a_s \cdot S_{\text{signal}}) / c_s}{\alpha \cdot \beta \cdot (h_p)^{\beta-1}} \quad (5.7)$$

The denominator of the formula is the allometric height-volume relation, derived from equation 1.4. Because the carbon allocation to height growth is dependent on the carbon gained by net photosynthesis, the carbon allocation to height growth can never exceed the carbon gained by net photosynthesis. If P_n is negative, no height growth occurs. However, whenever P_n is positive and the plant does grow in height, leaf area has to be reallocated. This brings costs and these can exceed the carbon available from net photosynthesis. After calculation of the leaf reallocation costs, it is evaluated whether the carbon balance is still positive or negative. Then extra leaf area is consumed or produced accordingly (see ‘carbon balance’ in this chapter).

Discussion

Carbon has an important structural and energetic role in plants. It is the compound by which organisms store and transfer energy (Mooney, 1972). The process of photosynthesis captures energy, which is stored in reduced carbon compounds until the energy is released through respiration. This energy is used to drive other important plant processes, for instance investments that enable the capture and subsequent utilization of other resources (Reekie & Bazzaz, 1987a). It is therefore logical to model plant growth and allocation processes on the basis of a carbon economy. Reekie & Bazzaz (1987b) showed that the carbon also tends to integrate the allocation patterns of other resources. Carbon is thus a relevant measure for allocation patterns in general.

The model described in this chapter can be used to simulate mechanistic growth of plants, on the basis of light capture. The inclusion of a carbon balance ensures that income and costs determine the growth concisely. The explicit crown shape is important

for accurately determining light capture. The model consists of four major elements: calculation of the light environment, the photosynthetic calculations, shape of the plant and the allocation program. All four elements can be altered or adjusted depending on the requirements of the simulation.

The allocation pattern of our model plants is hierarchical. Even though existing data can be interpreted in terms of hierarchical allocation pattern, there are virtually no studies that have investigated hierarchies explicitly (Worley et al., 2003). In some instances, explicit priorities in allocation to various plant organs have been shown in perennial plants (Suzuki, 2001). Although in many models the relation between life-history traits is implicitly assumed to result from alternative allocation of resources, explicit mechanistic models of this allocation process are few (de Jong & van Noordwijk, 1992). In our model, we use an investment pattern that seems obvious intuitively for annual plants. Nevertheless, the investment pattern to different plant organs like stem, leaf and roots can be altered to investigate fitness values for other allocation patterns.

It should be taken into consideration that a model with too many factors operating (and interacting) at the same time could become untraceable. It is therefore recommendable to limit the amount of interactions by only looking at the trait or process of interest and keeping other traits or processes constant. Some elements of plant growth have been omitted in this model, for reasons of simplicity. Roots have not been provided with a functional role in terms of nitrogen uptake or water uptake. An explicit storage for carbon is not included. Instead, a portion of the carbon from the leaves and roots can be used to account for a temporary negative carbon balance (Thomas & Sadras, 2001). Leaf turnover occurs whenever the plant grows in height by shedding leaves at the base of the stem and adding leaves at the top. Constant turnover of plant material is not explicitly included. Maintenance of standing biomass, however, is included. This implicitly incurs the cost of constant turnover of a fraction of the leaves and roots. To include a more realistic light environment, the model can be extended with a variable light climate throughout the season.

The model will allow for the evaluation of the fitness value of separate traits, ontogenetic investment patterns and plasticity. In addition, it can be used for the evaluation of the fitness of certain trait combinations. The model can be extended to a higher level of organisation, for instance competition between plants. The plants grow in response to the light that is captured over the height of the plant by the leaves. The light climate is determined by the extinction of light through the different leaf layers of the plants themselves. This allows for simulations on the ability of plants to withstand competition or ability to interfere. The model results can be used as a basis for game theoretic calculations, scaling up from within year performance to long-term year to year performance. Lastly, the model can be made spatially explicit. The model can be extended with a dispersal function, so plants can position their offspring in other vegetation cells. The effect of dispersal, competition and resulting pattern formation on the fitness of plants with different traits can be evaluated.

Appendix 1. The leaf area distribution formula

Formula 1.1 gives the leaf area distribution of model plants. The term $(x)^{p_1}$ determines the shape of the top of the plant whereas $(1-x)^{p_2}$ determines shape of the bottom of the plant. If p_1 and $p_2 < 1$, the leaf area distribution function is concave at both ends, if p_1 and $p_2 > 1$, the leaf area distribution function is hollow at both ends. It can be reasoned that if p_1 and $p_2 \rightarrow \infty$ the function is narrow (3a), whereas if the parameters approach zero, the function is broad (3b). The extreme value of the leaf area distribution function along the height of the plant is given by the ratio between p_1 and p_2 .

Extreme value of the LA distribution function
$$h_{ex} = \frac{p_1}{p_1 + p_2} \cdot h_p$$

If $p_1 > p_2$, the bulk of the leaf area is more at the bottom of the plant (3c). If $p_1 < p_2$, the bulk of the leaf area is more at the top of the plant (3d).

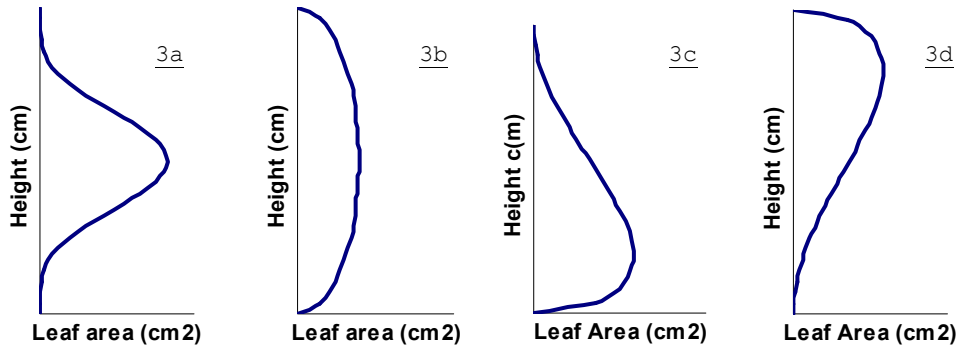


Figure 3. Different leaf area distributions as determined by the shape parameters p_1 and p_2 . In Figure 3a: $p_1 = p_2$ where $p_1 > 1$ and $p_2 > 1$. In Figure 3b: $p_1 = p_2$ where $p_1 < 1$ and $p_2 < 1$. Figure 3c: $p_1 < p_2$ where $p_1 < 1$ and $p_2 > 1$. In Figure 3d: $p_1 > p_2$ where $p_1 > 1$ and $p_2 < 1$.

Appendix 2. Calculation of h^*

Given below is the calculation of h^* , the point at which the leaf area change rate is zero with a given height growth rate. Differentiation of λ with respect to h_p gives:

$$d_{h_p} \lambda = d_{h_p} \cdot \left[p_0 \cdot L \cdot \frac{1}{h_p} \cdot \left(\frac{h}{h_p} \right)^{p_1} \cdot \left(1 - \frac{h}{h_p} \right)^{p_2} \right]$$

From this follows

$$d_{h_p} \lambda = p_0 \cdot L \cdot \left[-\frac{1}{h_p^2} \cdot \left(\frac{h}{h_p} \right)^{p_1} \cdot \left(1 - \frac{h}{h_p} \right)^{p_2} + \frac{1}{h_p} \cdot \frac{-p_1 \cdot h^{p_1}}{h_p^{p_1+1}} \cdot \left(1 - \frac{h}{h_p} \right)^{p_2} + \frac{1}{h_p} \cdot \left(\frac{h}{h_p} \right)^{p_1} \cdot p_2 \cdot \frac{h}{h_p^2} \cdot \left(1 - \frac{h}{h_p} \right)^{p_2-1} \right]$$

Which we can rewrite as:

$$d_{h_p} \lambda = p_0 \cdot L \cdot \left[\frac{1}{h_p^2} \left(\frac{h}{h_p} \right)^{p_1} \cdot \left(1 - \frac{h}{h_p} \right)^{p_2-1} \cdot \left[-\left(1 - \frac{h}{h_p} \right) - p_1 \left(1 - \frac{h}{h_p} \right) + p_2 \frac{h}{h_p} \right] \right]$$

To calculate h^* (the point on the stem height at which the leaf area change is zero) the equation must be set to zero. For the left-hand term this means that either p_0 , h_p , L must be zero or h equal to h_p . To find the point h^* somewhere at the height of the plant where leaf area change with height growth is zero, we substitute the term h/h_p with x and calculate for the right-hand term:

$$-(1-x) - p_1 \cdot (1-x) + p_2 \cdot x = 0$$

Solving this equation for x , this gives

$$x = \frac{p_1 + 1}{1 + p_1 + p_2} \quad \text{And hence } h^* \text{ is given by} \quad h^* = \frac{p_1 + 1}{1 + p_1 + p_2} \cdot h_p$$

Appendix 3. Symbols per section: Table of units

Section 1: Shape of the model plant

λ	Leaf area per height	$\text{m}^2 \text{ leaf} / \text{m height}$
L	Leaf area	m^2

CHAPTER 2

h	Height	m
h_p	Plant height	m
h_v	Vegetation height	m
p_0, p_1, p_2	Crown shape parameters	-
S	Stem volume	m^3
α, β	Stem shape parameters	-
R	Root weight	g

Section 2: Light climate

i_h	photon flux density at height	$\mu\text{mol photons/ m}^2/\text{s}$
α	Leaf inclination	degrees from horizontal
a	leaf absorption coefficient	-
i_{al}	photon absorption	$\mu\text{mol photons/ m}^2/\text{s}$

Section 3: Leaf and plant Photosynthetic rates

Φ	Quantum yield	$\mu\text{mol CO}_2/\mu\text{mol photons}$
P_{gl}	leaf photosynthetic rate	$\mu\text{mol CO}_2/\text{m}^2/\text{s}$
P_{ml}	leaf photosynthetic capacity	$\mu\text{mol CO}_2/\text{m}^2/\text{s}$
θ	Curvature	-
P_g	Gross plant photosynthetic rate	$\text{g C/ m}^2/\text{day}$
P_n	Net plant photosynthetic rate	$\text{g C/ m}^2/\text{day}$
R_m	Plant maintenance	$\text{g C/ g C mass/ day}$
r_{ml}	leaf maintenance constant	g C/ g C mass/day
r_{ms}	Stem maintenance constant	g C/ g C mass/day
r_{mr}	Root maintenance constant	g C/ g C mass/day
f_c	Seed allocation constant	$\text{g C/ g C net phot. prod.}$
F_m	Seed weight	g
L_c	Leaf carbon mass	g C
S_c	Stem carbon mass	g C
R_c	Root carbon mass	g C
c_l	gram carbon per unit leaf area	g C/ m^2
c_s	gram carbon per volume stem	g C/ m^3
c_r	gram carbon per root mass	g C/ g root
c_f	gram carbon per seed mass	g C/ g seed

Section 4: Growth and the carbon balance

r_l	Leaf growth respiration constant	g C/ g C leaf
r_r	Root growth respiration constant	g C/ g C root
r_s	Stem growth respiration constant	g C/ g C stem
r_f	Seed production respiration constant	g C/ g C seed

CHAPTER 2

c_{rl}	Leaf retrievable carbon	g C/ g C leaf
c_{rr}	Root retrievable carbon	g C/ g C root
C_{cf}	Seed carbon consumption rate	g C/ day
C_{cl}	Leaf carbon consumption rate	g C/ day
C_{pl}	Leaf carbon production rate	g C/ day
σ	Leaf /Root ratio	g root / m ² leaf
C_{cr}	Root carbon consumption rate	g C/ day
C_{pr}	Root carbon production rate	g C/ day
C_{ch}	Height carbon consumption rate	g C/ day
L_r	Leaf area shedding rate	m ² / day
L_p	Leaf area production rate	m ² / day
$C_{c\lambda}$	Leaf reallocation consumption rate	g C/ day

Section 5: The allocation program of the plant

a_s	Maximum allocation to height growth	g C/ g C net phot. prod.
S_{signal}	Shading signal	-
I_h	Total intercepted light per plant	μmol photons/ m ² / day
I_{hr}	Possible intercepted light	μmol photons/ m ² / day

**EXPLORING HEIGHT GROWTH TRAITS AS A MECHANISM
FOR COEXISTENCE**

Summary

We investigate whether different investments in height and leaf area can be a mechanism for coexistence between pairs of plant types competing for light. This question is addressed with the help of a mechanistic plant growth model. Within a season, contrasting plant types with a high and a low investment in height could coexist for a long period because of a temporal division in light usage. In contrast, types with an intermediate height investment quickly excluded both high and low investment types. Increasing similarity in the investment in height for competing types was cause for a longer period of coexistence, because of the overlap of leaf area and resulting interference. Thus, both limiting similarity and random drift processes could play a role in the community development of competing plants. We also studied the influence of frequency dependence. Negative frequency dependent feedback loops caused contrasting pairs of plant types to coexist in stable equilibrium. In this analysis, a very distinct pattern of coexistence was found between different types of height investment plants. The height investment determined whether, and with what range of height investment, plant types could coexist. These findings shed light on the role of leaf and height growth as possible mechanisms behind the coexistence of competing species.

Keywords: competition, allocation pattern, plant growth, mechanistic model, plant traits, height growth

Introduction

Light is usually the most important factor influencing the growth and development of plants in stands not limited by water or nutrients (Harper, 1977; Hirose and Bazzaz, 1998). Light is a unidirectional resource and photon flux density decreases exponentially with increasing depth in dense canopies (Monsi & Saeki, 1953). For this reason, light partitioning in a canopy is not symmetrical among individuals with different leaf and height traits (Hirose & Werger, 1995; Schwinning & Weiner, 1998; Anten & Hirose, 2001; Werger et al., 2002). Leaf area and height are important traits in the acquisition of light. All other traits being equal, a plant that is higher than its competitor can intercept more light in a stand with other plants. A plant with a bigger leaf area also will intercept more light if all other traits are equal. At the same time these plants have the dual advantage of overshadowing the subordinate plants.

During a growing season, competition for light can bring about variation in plant heights and patterns of leaf distribution over plant height in stands of vegetation (Weiner & Whigham, 1988; Schwinning, 1996; Schwinning & Weiner, 1998). These differences alone have been shown to allow for coexistence. Hirose & Werger (1995) and Anten & Hirose (1999) showed that short and tall plants could achieve similar light harvesting efficiencies per unit biomass. This could facilitate coexistence. Under the assumption of completely one-sided competition, Iwasa et al. (1984) found, using a static model, if crown thickness was thin enough, an infinite number of trees differing in height could coexist. In the same manner Huisman et al. (1999) found that a tall and subordinate species could coexist in a stable way.

But even though height and leaf traits at a single point in time can cause differences in instantaneous light interception, they do not necessarily sufficiently explain the differences in the total amount of light intercepted over the lifetime of a plant. Anten & Hirose (1999) already showed that the light harvesting efficiencies for plants of different heights were not static but varied over the course of a season.

The total light interception over a plant's lifetime is affected, in the first place, by the ontogenetic pattern of investment in height and leaf area. As biomass investments are drawn from the available pool of carbohydrates, it is clear that investments in leaf area cannot be used for an investment in height, and vice versa. Thus, investments in leaf area and height are under the restriction of an allocation trade-off (Givnish, 1982; Stutzel et al., 1988; van Hinsberg & van Tienderen, 1997; Anten & Hirose, 1999). This determines the shape of a plant and by doing so affects the light climate in the stand at the same time. In dense stands, the height and leaf area of neighbours also determine the light climate experienced by any individual in the stand. In addition, competition for light affects growth form in terms of leaf area and height, and growth form mediates competitive interactions (Weiner & Thomas, 1992; Weiner & Fishman, 1994, Anten & Hirose, 1998) by modifications in the light climate. The interplay between plant shapes, light climate and growth makes the light interception of plants dynamic rather than static.

The plant's allocation pattern combined with the interaction with neighbouring plants largely affects the shape of the plant and plant performance at any point in time (Figure 1).

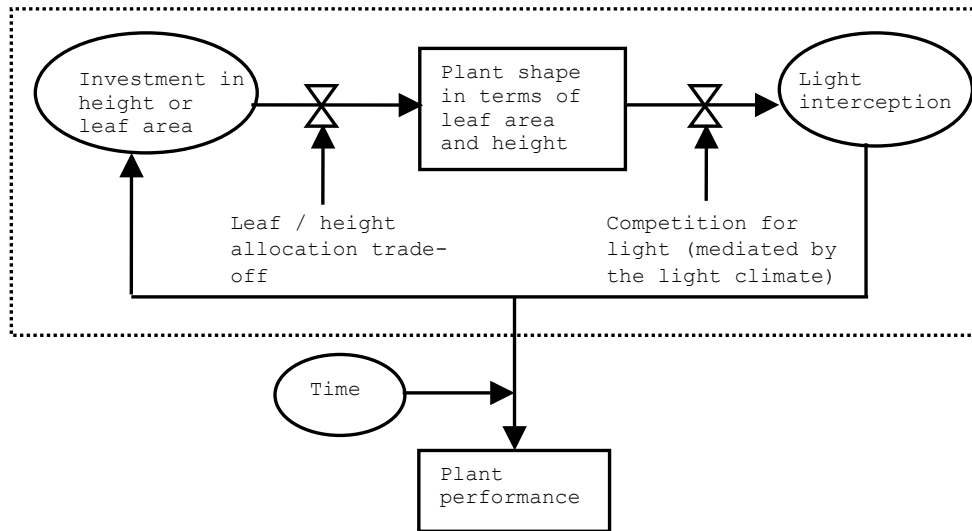


Figure 1. Flowchart of lifetime plant performance and influences, as treated in this chapter.

In an evolutionary context, selection pressures will act on the physiological mechanisms that determine differences in height and leaf area; namely the leaf and height investment patterns. Consequently, to elucidate the role of light harvesting mechanisms behind coexistence, the question arises whether differences in height and leaf area investment history, rather than momentary differences in height and leaf area, affect coexistence. To compete successfully in the course of years, the leaf and height investment patterns would have to be adaptive. Considering the persistent diversity in plant shapes that we observe in nature (Werger et al., 1987) the question can be asked whether different height and leaf area investment patterns do indeed affect the plant's ability to persevere in vegetation and coexist with other plant types. Yokozawa et al. (1996), investigating coexistence during one generation of competing plant types, showed that initial height affected species coexistence patterns when comparing model trees with spherical and conical crowns. However, their fitness measure, namely the time to death, is rather trivial and does not say much about the possible success of types over generations.

To be able to include and analyse the effect of investment patterns on the performance of plants in competition for light, we have chosen to do a theoretical study. Theoretical studies enable us to gain insight on the effects of investment patterns in circumstances that are simpler and more traceable than the real life situation. An

appropriate way to theoretically analyse the non-linear growth dynamics of interacting plants is to make use of a mechanistic model, as simple *a priori* functions are less capable to capture the behaviour of the non-linear dynamics in asymmetric competition.

In this chapter we discuss the results of the simulations on interacting plants with such a mechanistic model. Throughout the chapter the central question will be whether coexistence of plants with different height investment strategies is possible. We consider plants that invest different proportions of their net photosynthetic production in height growth over time. Furthermore, this investment trades off with investment in leaf area growth. First, we analyse plant performance and coexistence patterns within a growing season with different pairs of plant types that differ in height investment. Second, we study the frequency dependence of coexistence patterns of pairs of plant types, while keeping density constant.

Method

A complete description of the mechanistic plant growth model is given in Chapter 2. Here we give only a brief discussion of the most important features of the model.

All plant types consist of three basic structures: leaves, roots and a stem. Aside from these structures, the plant stores carbon to be used for seed production. At the end of the simulation period, total carbon storage is a measure for the lifetime opportunities of each plant to intercept light and store carbon for seed production. Although it has been proven that in theory a plant should make a clear switch to investment in reproduction rather than investing simultaneously in vegetative growth and reproduction (Cohen, 1971; Iwasa, 2000), in practice plants switch gradually (King & Roughgarden, 1983; Kozlowski, 1992). For reasons of simplicity, we use a constant partial storage of carbon for seed production. The fitness now is a direct measure of lifetime net photosynthetic production and therefore closely related to lifetime-produced biomass. Each plant type starts with an initial leaf area, root mass, and height (see Table 4 in the appendix for initial values). From the start of the simulation, the plant intercepts light, photosynthesises and grows. There is a particular order in which the carbon gained by photosynthesis is partitioned. First, plants use carbon for maintenance respiration, depending on their structural mass. Of the remaining carbon, a fixed percentage is stored that can later be used for the production of seed mass. Next, the requirements for vegetative growth are met. With the construction of vegetative structural mass, a constant amount of carbon per unit mass is respired. When plants grow, the allocation of carbon to the stem to grow in height has priority. The distribution of leaf area over the height of a plant is described by a function. A consequence of the leaf distribution function is that, with an increase in height, leaves at the base of a plant are discarded while leaves at the top have to be newly produced. It is assumed that the carbon imbedded in the structural mass of leaves and roots is only partly retractable. This means that the reallocation of leaves with height growth implies an extra cost. Whatever carbon is left after height growth is invested in leaf area and root mass in some constant proportion.

Obviously, plants cannot spend more carbon than they have received. If the carbon balance after either maintenance or height growth is negative then leaves and root mass are shed. The retractable carbon from these leaves and roots is used to pay for the costs, until the costs are again equal to the total carbon spent. If the mass of either leaf or root structural mass is zero, plants are considered dead.

The steady state is the point at which the costs of maintenance equal the carbon gained in gross photosynthetic production. As a consequence, net photosynthetic production is zero and growth is not possible. A plant will have no further possibilities to store carbon for seed production. This is a good point to compare lifetime storage of carbon of plants with different height growth. We take the simulation period such that single isolated plants of all different types are able to reach the steady state. This time span (700 simulation steps) is taken as the standard simulation period. We do not link the simulation period to an exact time in a real growing season, for many processes that could alter the time to reach steady state are not taken into account to keep the model results tractable. For instance, turnover of leaves and roots would increase the costs for plants and shorten the period of growth. Another factor is the light climate, which is constant in the model but in reality will decrease towards the end of the season, thus reducing lifetime light capture and the period of growth. In this view, the actual period in which plants can reach steady state in our simulations is rather irrelevant. The assessment of plant performance at steady state is another matter. We will discuss the consequences of assessing the performance plants at different stages of growth in Chapter 4. Initial plant parameters for plant shape, photosynthesis and growth were set to approximate average characteristics of herbaceous plants (see Table 4 and Table 5 in the appendix).

The height growth strategy considered in this chapter is one in which plants invest a constant proportion of carbon in height growth. Types within this strategy divert different fixed fractions of gained carbon to the stem part to grow in height.

We distinguish types that invest in height growth from 2.5% up to 47.5% of the net carbon gained by photosynthesis, increasing in steps of 5% in each type. Listed in Table 1 are the height investment types that will be used throughout this chapter.

Table 1. Constant percentage of net photosynthetic production invested in height growth for all distinguished height investment types.

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7	Type 8	Type 9	Type 10
(%) Height Investment	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5

Results

Single Isolated Plants

In model simulations with isolated plants, height is presumed to have no advantages in terms of light interception. It is probable that the maintenance of stem biomass will only be a disadvantage because of the extra costs it implies. Considering this, at the end of the simulation period a decreasing fitness with an increasing investment in height is expected in solitary plants. The type with the lowest investment in height is expected to have the highest fitness. Figure 2 shows the final attained height, leaf area and seed mass at the end of the simulation period for the different types.

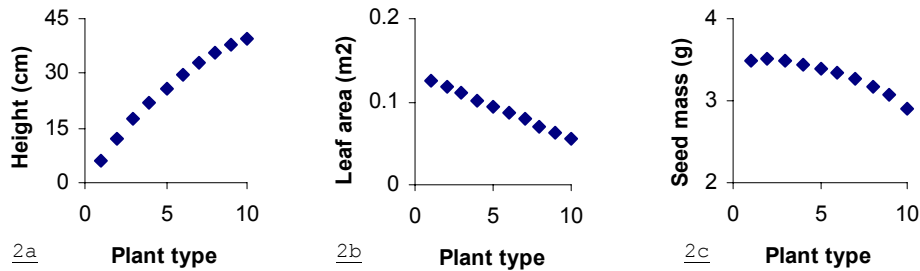


Figure 2: Height (a) leaf area (b) and seed mass (c) of isolated plants of different types, after simulation. Percentage of net photosynthetic production invested in height growth of plant types: 1=2.5%, 2=7.5%, 3=12.5%, 4=17.5%, 5=22.5%, 6=27.5%, 7=32.5%, 8= 37.5%, 9=42.5%, 10=47.5%.

Plant types that invest a larger proportion of carbon in height than the types considered in Figure 2 (see also Table 1) are eventually lower than plant types that invest less in height. There is a simple explanation for this. The more a plant invests in the stem part, the less is invested in leaf area (Figure 2b). Cippolini & Schultz (1999) found that stem elongation was costly for growth and fitness in phenotypically manipulated plants. They found that the fundamental mechanism producing such costs is allocation of resources away from resource harvesting roots and leaves to support the increased stem growth, which is consistent with our assumption. With a small leaf area the plant cannot intercept much light. Consequently, there is little carbon from net photosynthetic production available for overall growth, and the plant has a smaller stature as a result. Obviously, these plants would perform poorly in competition with other plant types. We include only those plant types that actually increase in height with an increasing investment in height, relative to the height investment type that precedes them. Figure 14 in the appendix shows the growth of single isolated plants of every considered type. Figure 2c shows the seed production from stored carbon of the different types. Surprisingly, the type possessing the lowest height investment does not have the highest fitness. This implies that, for single

plants, the most beneficial strategy is to invest at least some carbon from net photosynthetic production in height. The explanation for these results lies in the leaf area that was produced by the plants. Plants that invest little in stem are able to produce a very large leaf area. The associated increase in self-shading decreases the income per unit leaf area while the maintenance costs per unit leaves (and associated roots) remains constant. Single isolated plants with a moderate height investment have the best performance for they experience less self-shading and have no large stem respiration costs. In a real situation, single isolated plants will also benefit from a slight stem investment. With this investment they can position leaves in such a way, for instance sideways, that the leaves shade each other to a lesser extent. Although this phenomenon is not explicitly included in our model plant, the quantitative results coincide.

To test whether the model produces results within an acceptable range of values (e.g. plant size and ratio's) we look at the characteristics of the different types of model plants at the end of the simulation period. As can be seen in Table 2, ratios such as leaf area ratio and shoot root ratio are within ranges that can normally be found in field or experimental conditions. Absolute characteristics such as weight, height and leaf area are also within the right order of magnitude.

Table 2. Range of plant characteristics for single plants of different height investment types after reaching the steady state. See Table 4 and 5 in Appendix 1 for more details. See Table 1 for a description of distinguished types.

Characteristic	Range	Unit
Plant weight	5.9 - 6.5	g
Leaf area ratio	9.4 - 19.4	cm ² /g
Shoot / root ratio	2.1 - 5.4	g/g
Leaf area	0.055 - 0.126	m ²
Leaf area index	5.5 - 12.6	m ² /m ²
Height	5.8- 39.5	cm

Figure 2c showed that the seed output (and thus fitness) does not differ more than 20% between plants of different height investment types. However, competition might change this drastically. In the next section the influence of competition on the performance of the different types will be explored.

Competition between types

In solitary plants, the plant types varied maximally 20% in final seed mass at steady state (Figure 2c). Moderate height investment plants (type 2) performed somewhat better than

the other types. In this section we will explore how these plant types fare in pair-wise competition. When plants of different height investment strategies compete, the success of a plant depends on its own inherent strategy but also on the strategy of the opponent. The question we address is whether one height investment type is superior to all other height investment types or if the success depends on the type of opponent.

In the literature, there are roughly two prevailing concepts regarding performance and coexistence of plants in competition. One concept is based on the competitive exclusion principle and states that, when two plant types compete for a shared resource, the best competitor will eventually exclude the other (Gause, 1934; Abrams, 1983). Competition should be most intense between the most closely related forms and should therefore lead to the exclusion of one type by another, so these types coexist less often than expected by chance (Aarssen, 1989). Consequently, species should be dissimilar to some degree, so that both can occupy a different niche and avoid competition (Silvertown & Lovett Doust, 1993). The other concept states that similarity of species can delay competitive exclusion for a long period of time, because neither of the competing species is strong enough to exclude the other (Hubbel & Foster, 1986; Chesson & Case, 1986).

For this analysis we use plants of types that have a low, medium or high investment in height growth. These are types 1, 5 and 10 respectively (for a description of types, see Table 1). The plants compete in an area of ten by ten centimetres. Horizontally, leaves are spread over the total surface of the cell area. The leaves of both competitors are homogeneously mixed. Vertically, the leaf position per plant is determined by the height of the plant and the leaf area distribution function.

It can be argued that both high and low height investment types have an advantage. A plant of type 10 will have an advantage over a plant of type 1 because it can intercept photosynthetic active radiation while shading the plant of type 1. At the same time, a plant of type 1 has an advantage because it does not have to maintain much stem biomass and is able to produce a large leaf area. Because of the advantages resulting from both height investment strategies, we expect that a low height investment plant (like a plant of type 1) in the presence of a high height investment plant (like a plant of type 10) will be able to persevere for a long period of time.

In competition with a plant of type 10, we expect a plant of type 5 to perform less than a plant of type 1. A plant of type 5 will have more maintenance costs from produced stem mass and will be shaded nonetheless by the plant of type 10. Because of the asymmetry of competition, these negative effects of shading will be enhanced in time while costs for stem maintenance remain the same. It is hypothesised that a type 5 plant will not be able to withstand the competitive pressure for long.

For a plant of type 1 in competition with a plant of type 5, we expect the plant of type 1 to not be severely over shadowed and thus not reduced in growth. This is because a plant of type 5 has a lower height as compared to a plant of type 10. A plant of type 1 may even be fitter than a plant of type 5. The latter will have only a small advantage in light capture resulting from a slightly bigger height.

Plants that are more similar in terms of height growth investment will experience more intense competition and the weaker competitor will be severely suppressed. Thus, on the basis of performances of single isolated height investment types in the previous section, we hypothesise in the line of thinking of the competitive exclusion principle. More dissimilar plants will exhibit a longer period of coexistence. In terms of fitness we expect the pair that is most dissimilar to have the most similar performance.

Figure 3 shows the height and leaf area developments and seed production of competing plants of type 1 and 10.

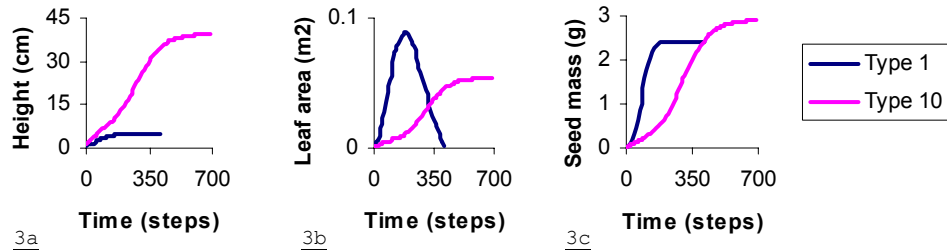


Figure 3. Height investment type 1 in competition with height investment type 10. a: Height development. b: Leaf area development. c: Carbon storage for seed. See Table 1 for a description of plant types.

Looking at the results of the simulation of competition between height investment plant types 1 and 10, it can be seen that the type 1 plant performs well initially. Because plants of type 1 can invest a lot of carbon in leaf area, the leaf area quickly develops (Figure 3b). With this large leaf area the plant of type 1 can intercept much PPFD and can rapidly produce seed mass (Figure 3c). However, when steady state is reached towards the end of the simulation, the plant of type 10 has the best performance. This plant invests in height and therefore has a rapid height growth (Figure 3a). Nevertheless, its leaf area development is slow (Figure 3b) and it does not over-shadow the plant of type 1 until late in the simulation. Although the plant of type 1 dies, it indeed perseveres a long time under the plant of type 10 and attains a rather similar storage for seed production (Figure 3c). This is what we expected from this simulation.

It can be concluded that there are separate temporal niches for the two types. First type 1 performs best and rapidly produces seed. By the time the slow-growing type 10 shades type 1, the latter already has a large seed mass production.

For the next simulations, a medium height investment plant type 5 is put in competition against the extreme height investment types. Figure 4 shows the developments of type 5 versus a plant of type 10 and Figure 5 shows the development of competing plants of type 1 and 5.

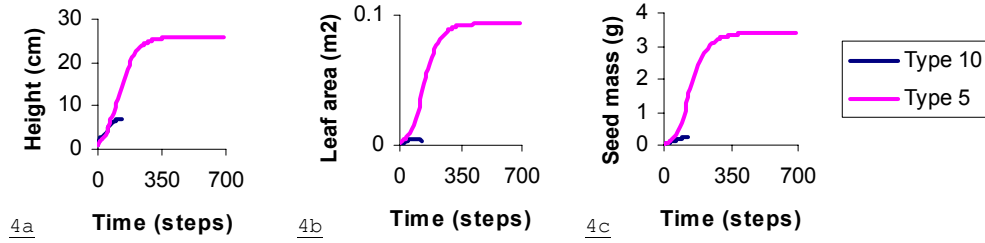


Figure 4. Height investment type 5 competing with type 10. a: Height development. b: Leaf area development. c: Carbon storage for seed. See Table 1 for a description of plant types.

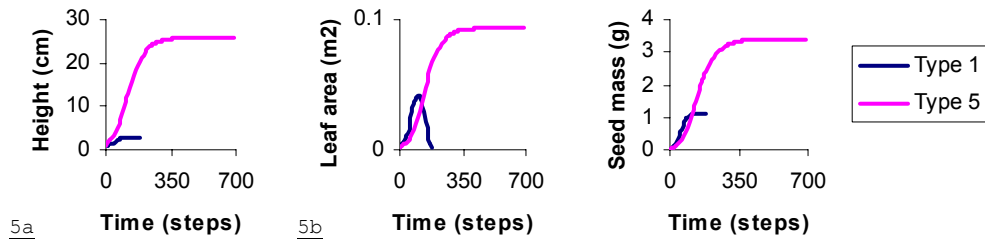


Figure 5. Height investment type 5 competing with type 1. a: Height development. b: Leaf area development. c: Carbon storage for seed. See Table 1 for a description of plant types.

Interestingly, in contrast to our hypotheses on the performance of medium height investment types, Figure 4 shows that a plant of type 5 rapidly excludes a plant of type 10 instead of the other way around. Figure 5 shows that the type 5 plant excludes the type 1 plant very quickly as well. It seems that, in contrast to our expectations, a plant of type 5 is the more successful plant type in our simulations on pair-wise competition.

The origin of our results lies in the fact that a plant of type 5 interferes with a plant of type 10 as a result of a more advantageous combination of costs and benefits. The distribution of its leaf area over the height of the plant as we consider it in our model, is an important determinant of the outcome of the simulations. Plants in our model have their leaf area from the bottom to the top of the stem. Therefore there is always a degree of overlap in the leaf area of competing individuals. While (initially) it is not severely shaded, a plant of type 5 produces a considerable amount of leaf area as well as height. With this combination of height and leaf area, a plant of type 5 interferes with the light interception of a plant of type 10 to such a degree that the latter cannot produce the leaf area it would produce without the plant of type 5 as a competitor. This reduces the light

interception for type 10 while its costs remain the same. Consequently, its growth rate is less. This enables the type 5 to grow further and exclude type 10. In the case of competition between type 5 and type 1 plants, a plant of type 5 shades the low height investment type at an earlier stage than a plant of type 10 does because it can produce leaf area at a higher rate. As a consequence, a plant of type 5 excludes a plant of type 1 fast, more so than a plant of type 10.

In the light of these new insights, we can make a new prediction for different height investment types. With similar height growth patterns and consequent leaf area overlap, plants compete more intensively for light. This interference reduces the height and leaf area growth of the better competitor. The weaker competitor is therefore less over shaded and able to store more carbon for seed production. Also, it can persevere for a longer period of time. In the case that two competing plant types are totally similar, it is obvious that neither one will be able to displace the other. Depicted in Figure 6 are competing plants of more similar types.

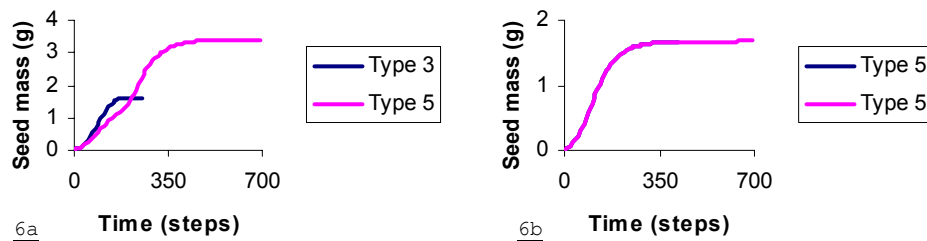


Figure 6. Carbon storage for seed production of pairs of height investment types in competition. a: Type 5 competing with type 3. b: Type 5 competing with type 5. See Table 1 for a description of plant types.

Indeed, when compared with Figure 5c, Figure 6a and b show that plants of subordinate types can persevere longer and make more seed accordingly if the competing plants are more similar. In the extreme case of total similarity, the plants coexist indefinitely.

We can ponder a bit on the population development of the pairs in each simulation. If one type of a pair produces more seed, it can be expected to increase in frequency faster than the other type. With a change in frequency the conditions for coexistence might change drastically. Competing pairs of types that have a more or less similar seed output at the end of the simulation period will differ slowly in frequency over the course of years. We can state that types with a separate temporal niche (like plants of type 10 and 1) will be able to coexist for a long time. Also types that have a similar height growth pattern produce more similar amount of seed mass and have a prolonged period of coexistence. If we assume some limit to the carrying capacity of the environment, a difference in seed output, however small, will eventually lead to a disproportionate

increase of the one type at the expense of the other (see models by Lotka (1925) and Volterra (1928). To get a stable coexistence between plant types it is necessary that the increase of the dominant type relative to the subordinate plant comes to a stop at some point in time. We need a mechanism that will bring about some feedback loop that affects population development of the dominant type negatively or the population development of the subordinate type positively. In the following paragraphs we will investigate whether frequency dependent phenomena can provide such a mechanism.

Plants competing at different frequencies: De Wit replacement series

In the previous section, the possibilities of coexistence within a season were discussed. Between pairs of plant types there was a large variety in fitness. Nonetheless, we came to the conclusion that stable long-term coexistence would not easily occur in stands with pair wise competition as defined in the previous section. It is possible that frequency dependent phenomena will provide a mechanism that does enable different types to coexist indefinitely.

To investigate the influence of frequency on the outcome of competition, pairs of plant types that differ in their investment in height are simulated competing at different frequencies. For this purpose we use a replacement series according to de Wit (1960). Within a fixed period of simulation time, the production of seed mass for each combination is simulated. The density of competing plants is kept constant at 200 plants per square meter to keep simulation results comparable with the pair-wise simulations in the previous paragraphs. Because in the de Wit replacement series more plants are competing, we enlarge the cell size to achieve similar densities. The number of individuals that compete per type, per simulation, is shown in Table 3.

Table 3. De Wit replacement series. Frequencies per type per simulation. See Table 1 for a description of types. The number of individuals is between parenthesis.

Simulation	1	2	3	4	5	6	7	8	9
Plants type A	0 (0)	0.125 (1)	0.25 (2)	0.375 (3)	0.5 (4)	0.625 (5)	0.75 (6)	0.875 (7)	1 (8)
Plants type B	1 (8)	0.875 (7)	0.75 (6)	0.625 (5)	0.5 (4)	0.375 (3)	0.25 (2)	0.125 (1)	0 (0)

After the standard simulation period of 700 time steps, we have the seed output per individual per combination. We calculate the total seed output S per type t at frequency f as:

$$\text{Total seed of output plant type} \quad S_{if} = s_{if} \cdot n_t \quad (3.1)$$

in which s_{if} is the seed output per plant of plant type t at that particular frequency and n_t is the actual number of individuals of plant type t .

The performance (P_t) relative to the other plant at the particular frequency is calculated as:

$$\text{Relative performance of plant type } t \quad P_t = \frac{S_{if}}{S_f} \quad (3.2)$$

in which S_{if} is the total seed output of the plant type and S_f is the total seed output of all competing plants in that combination. For all combinations, the performance of a plant type relative to the opponent is plotted against the frequency of the plant type. This results in a 'seed output curve', which shows a plant type's performance, in terms of seed output, relative to the opponent plant type when competing at different frequencies.

For any seed output curve (see Figures 7 for examples) it can easily be derived whether or not coexistence is possible (Inouye & Schaffer, 1981). At intersections with the line with slope 1, the relative performances for both competing types are equal. Neither will change in frequency, and thus coexist. The point where the actual seed output curve crosses the line with slope 1 is called the equilibrium point. This point can be stable or unstable. An unstable equilibrium means that the frequency developments of the competing plants will move away from the equilibrium point if there is a slight disturbance that changes the frequency distributions. One of the types will displace the other, depending on the direction of the disturbance. A stable equilibrium means that if there is a deviation away from the equilibrium point, the frequencies of plant type will always return to the equilibrium. This type of robust coexistence is what we are looking for.

If the relative seed production for a type is above the line with slope 1, it means that the type produces relatively more seed than its opponent and will increase in frequency. If the relative seed production is below the line with slope 1, the type will decrease in frequency. If the relative seed production goes from positive at low frequencies to negative at high frequencies (see Figure 7a), iterations will always go towards the equilibrium point and stable coexistence is possible. Otherwise, if the relative seed production goes from negative at low frequencies to positive at high frequencies (see Figure 7b), iterations will always move away from the equilibrium point and the equilibrium is unstable. In a more formal way, one can look at the slope of the curve. If the absolute value of the slope of the relative performance curve is between one and zero while crossing the curve with slope 1, the equilibrium point is stable (Yodzis, 1989).

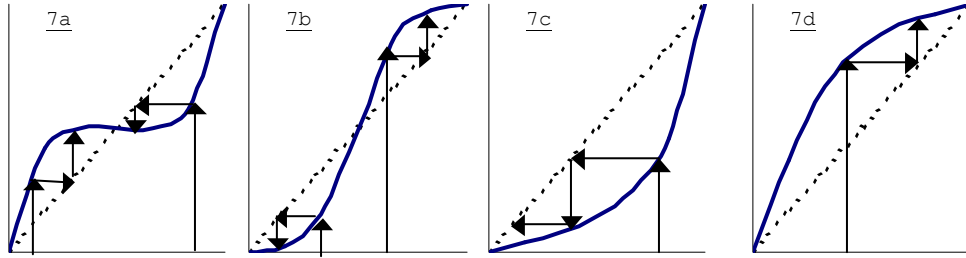


Figure 7. Iteration graphs for different curves. On the x-axis: relative frequency (0 to 1). On the y-axis: relative performance (0 to 1). Figure a: Stable equilibrium. Figure b: Unstable equilibrium. Figure c and d: No equilibria.

For the first simulation, plants of height investment type 7 compete with plants of type 2 in the combinations shown in Table 3. Depicted in Figure 8 is the performance of type 7 plants at different frequencies relative to type 2 plants.

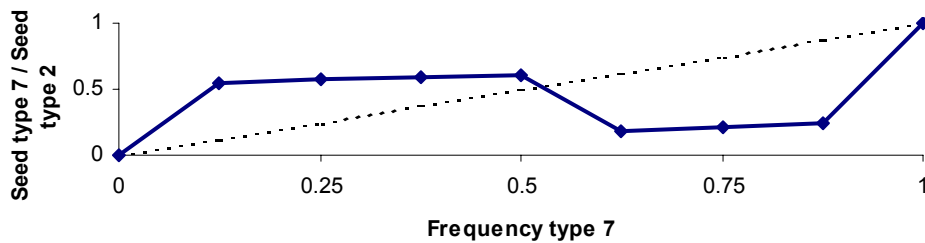


Figure 8. The relative performance of type 7 plants, competing at different frequencies against type 2 plants. See Table 1 for a description of types. See Table 3 for amount of individuals of competing plant types at each frequency.

At a low frequency of con-specifics, the total seed output of type 7 plants lies above the line of equal seed production. Hence plants of type 7 will increase in frequency. At high frequency of con-specifics, however, the total seed output of type 7 plants lies below the line with slope 1. This means they will decrease in frequency. From this, it can be derived that plant type 2 and 7 are able to coexist. There is a stable equilibrium. Type 7 plants perform relatively well at a high frequency of type 2 plants. And, quite the reverse, plants of type 2 perform relatively well at a high frequency of plants of type 7.

To explain this negative feedback, we take a look at the performance of individual plants in terms of height, leaf area growth and the resulting seed mass

production of individuals of both type 2 and 7 in two different frequency combinations. Figure 9 and 10 show the performance per individual of competing plants of types 2 and 7. Figure 9 depicts the growth of individuals of both types at a low frequency of type 7 plants. Figure 10 depicts the growth of individuals of both types at a high frequency of type 7 plants.

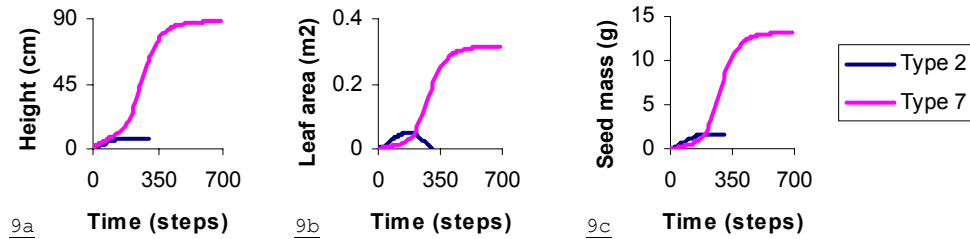


Figure 9. Performance per individual of competing height investment types 2 and 7 in an environment consisting of a low frequency of Type 7 plants. a: height growth. b: Leaf area development. c: Carbon storage for seed mass production. For a description of types see Table 1.

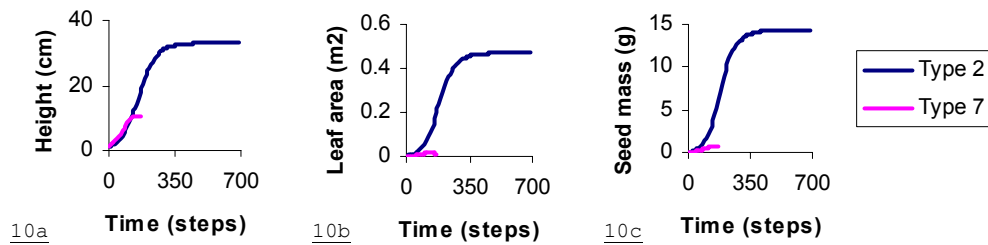


Figure 10. Performance per individual of competing height investment types 2 and 7 in an environment consisting of a high frequency of Type 7 plants. a: height growth. b: Leaf area development. c: Carbon storage for seed mass production. For a description of types see Table 1.

In an environment with a low frequency of type 7 plants (Figure 9), type 7 plants do not have to compete for the available light with con-specifics. Therefore they encounter a more profitable light climate when growing in height. Plants of type 7 are able to produce leaf area (Figure 9b) with which they can shade type 2 plants eventually. Seed production of type 2 plants stops while seed production of type 7 plants continues (Figure 9c).

In an environment with a high frequency of plants of type 7 (Figure 10), type 7 plants outgrow type 2 plants initially in terms of height (Figure 10a) but their leaf area growth is small (Figure 10b). Making costs on account of the stem part only pays off

when a more profitable light climate is encountered when investing and growing in height. Because the light climate is shared with so many con-specifics, this is not the case. Eventually the type 7 plant has so little carbon to invest that height growth stops. Seed production is very small (Figure 10c). Type 2 plants, in turn, have the ability to produce a lot of leaf area because they are not severely shaded.

In conclusion, the explanation for the negative feedback loop lies in the fact that high height investment plant types like type 7 are limited at high frequency because light competition with con-specifics limits their growth.

Types 2 and 7 achieve an equal seed production at a frequency of 55% of type 7 plants (see Figure 8). To explore where the position of this equilibrium point will lie in competition with other plant types, the height investment of plants of type 7 is increased from 32.5% to 37.5%. This is the height investment of type 8. Figure 11a shows that the equilibrium point shifts towards the left. In other words, it lies at a lower frequency of high height investment types. This can be explained by the fact that the higher investment types have more costs from the increased stem investment. The type can only perform well if there is a lower amount of plants of the same height growth competing for light. If the height investment for type 7 plants is decreased, the equilibrium point of course shifts to the right (Figure 11b).

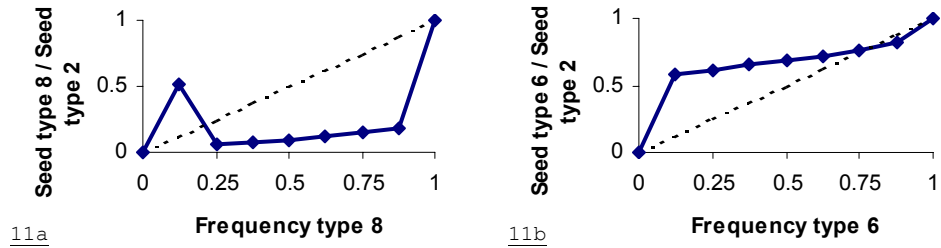


Figure 11. The relative performance of RHI strategy type 8 plants (a) and type 6 plants (b) competing against type 2 plants at different frequencies. See Table 1 for a description of types. See Table 3 for amount of individuals of competing plant types at each frequency.

Reducing the height growth of type 2 plants shifts the equilibrium to the right, towards a higher equilibrium frequency of type 7 plants. Increasing the height investment for type 2 plants to a type 3 shifts the equilibrium to the left. Because these plants now can reach a greater height than the original type 2, they interfere more with type 7 plants. The latter perform worse, and can only perform well with lower competition of con-specifics.

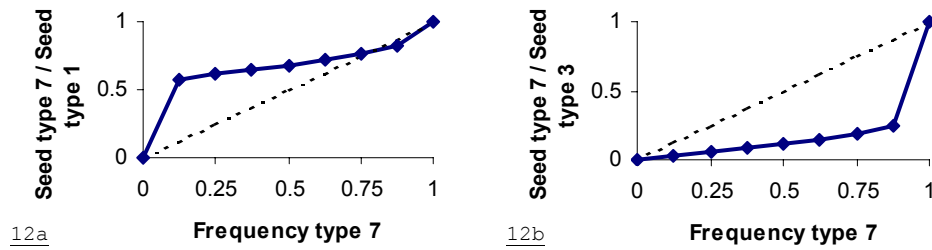


Figure 12. The relative performance of height investment type 7 plants, competing against type 1 plants (a) and type 3 plants (b) at different frequencies. See Table 1 for a description of types. See Table 3 for amount of individuals of competing plant types at each frequency.

Following these lines of reasoning it is logical that no coexistence occurs if the height investment of either competitor is increased or decreased too rigorously. In the competition between type 7 and type 3 (Figure 12b) there is already no more coexistence. Because of their beneficial cost / income ratio, type 3 plants perform so well that type 7 plants are severely limited already at very low frequency. As a consequence, type 3 plants displace type 7 plants at any frequency and thus are outside the range of coexistence with plants of types 3.

Taking the whole range of height investment types and exploring the possibilities for coexistence, something interesting appears. As predicted, extremely contrasting types can coexist. Counterparts can cover a range of height investments. Outside the range, there is no coexistence and from any starting frequency, one type eventually will displace the other type. When the contrasting height growth types are chosen more towards the mid position of the range of height investment types, the range of height investment at which coexistence occurs becomes narrower. This is because closer to one another, the plant types are more similar and mutual interference is bigger because of increased leaf area overlap. Plant types that have a relatively large height investment are more susceptible for a decrease in light availability by the presence of con-specifics. To put it differently, plant types that are very close to the mid position in the range of height investment, and thus very similar in height investment strategy, are still able to coexist. However, the range of height investment with which coexistence can occur is very narrow. At the exact mid position in the range of height investments, there is no possibility of coexistence. Plants of this height investment perform better than either higher or lower height investment strategies. Figure 13 shows some examples of the ranges and patterns in coexistence possibilities between pairs of plant types that differ in height investment. For each simulation a touchstone plant type (called a focal type) is distinguished. It is investigated what range of different height investment types is able to coexist with this focal plant

type. In Figure 13, the focal type and the range of height investment with which it can coexist are depicted horizontally.

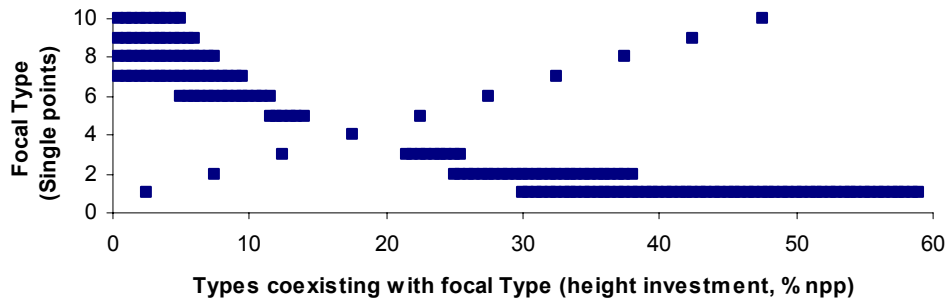


Figure 13. Coexistence pattern of competing height investment types. In horizontal direction are focal plant types (dots) and the range of plant types (bars) that are able to coexist with this type. For a description of types, see Table 1.

Although we demonstrate coexistence between many combinations of different height investment types, the question remains if we can get more than two types of plants to coexist. In the next chapter it is explored what happens if more types are allowed to compete.

Discussion

With help of a mechanistic plant growth model, we explored the possibilities for coexistence between pairs of plant types, within a season as well as on the long term. The plant types differed in their proportion of carbon from net photosynthetic production that was allocated to height growth. The investment in height growth traded off with the investment in leaf area. Types with a large investment in height growth had a fast height growth but slow leaf area growth. In contrast, types with a small investment in height growth had a slow height growth but fast leaf area growth.

As regards to coexistence within a season, we found that plants with both similar and dissimilar patterns of height investment could coexist for a long period of time. These types could attain a similar fitness as well. The niche differentiation theory predicts that coexistence can occur when plants can reduce competition by differing in their ways to exploit their environment (Silvertown & Lovett Doust, 1993). We found this phenomenon occurring in our simulations. Types with a small investment in height growth used the early part of the season for efficient light capture. These types could swiftly produce a large leaf area and this enabled the types to sufficiently intercept light. Additionally, they

were not yet severely shaded by the type with larger investment in height growth because its leaf area developed slowly. Types with large height investment gained the advantage from their greater height later in the season. For this type it took some time to increase its leaf area, sufficiently intercept light and to over shade the low height investment plant. Types thus could achieve a similar fitness because of a separation in the timing of light capture. Anten & Hirose (1999) found a similar pattern for light capturing efficiencies in their field study. In fact, a corresponding phenomenon is apparent in the seasonal development of the understory vegetation in our deciduous forests of the temperate zone (e.g. Werger & van Laar, 1985). The low understory plants start growth early in the season before the canopy above closes.

On the other hand, plants that were increasingly similar in their height investment pattern coexisted for a long period of time as well. Also they achieved a similar fitness. This agrees with the random drift theory that predicts that similar plants will not be able to exclude each other and therefore coexist (Hubbel & Foster, 1986; Chesson & Case, 1986). When height growth was more similar in our plant types, the overlapping leaf area between the two plants was larger. This caused the plants to interfere more strongly. The dominant plant remained smaller over its lifetime because of this competition. It could suppress the subordinate plant to a lesser extent. The assumption that similar plants will experience the strongest competitive pressure and therefore will exclude each other fast (Aarssen, 1989) is not valid in the competition for light. The results of our model simulations on the competition for light agree with both the theory of niche differentiation and that of random drift. The niche differentiation theory is apparent in a temporal separation of use of the available light. The random drift theory is apparent in the increased interference between types with a more similar height investment pattern. This reduces growth of the dominant type and relieves some of the competitive pressure for the subordinate type. Both mechanisms cause a more or less equal fitness between pairs of types.

In our simulations the ability to interfere was greatest for plants that invested more or less the same amount in height as in leaf area. The height of these plants gave them a better access to light, while the leaf area enabled them a relatively good light interception. These plants outcompeted plants that could attain a larger height (but produced a small leaf area) as well as plants that could attain a larger leaf area (but remained lower). Thus, height and leaf area are both very important for determining competitive strength of plant types competing for light. It might seem surprising that an intermediate height grower generally wins the competition in our simulations. This is especially so because height is often regarded as a measure of the competitive strength of plants (e.g. Gaudet & Keddy, 1995; Weiner & Thomas, 1992). However, leaf area is another important determinant of competitive strength (Mohktari et al., 2002; Weiher et al., 1999; Keddy et al., 2002). Because height investments trade off with investments in leaf area, the two traits should not be seen separated in their effect on competitive strength. Possibly, the role of height *per se* in determining the competitive strength is less important than generally assumed. Light interception (determined by plant height combined with leaf area) will be a better measure (Berntson & Wayne, 2000). One reason

why height is assumed important for competitive strength is because it is viewed in the following way: ‘...taller plants shade shorter plants but not vice versa’ (e.g. Falster & Westoby, 2003). This statement is only true if the crown of one plant is completely above that of the other plant. This strict separation of crowns will not occur very often. Almost always there will be some measure of leaf area overlap (Yokozawa & Hara, 1992; Geritz, 1995). We have shown that, when leaf area of plants overlap to some extent, a shorter plant can even shade a taller plant more than the other way around, given that the first has considerably more leaf area than the latter.

Pairs of competing plants with different height growth investment could stably coexist on the long term as a consequence of a negative frequency dependent phenomenon. At low frequency, most plants were of low stature and plants with a large investment in height had access to a favourable light climate. In this way the costs for height growth could be easily met. At high frequency, most plants had a large investment in height and these had to compete for the available light. As a consequence, light interception per plant with a large investment in height was less. Nevertheless, the costs for height growth per plant remained the same. In these circumstances, plants with large investment in height growth had less carbon available for leaf area production. Therefore plants with a small investment in height growth were less shaded and performed better than the plants investing more in height growth. Non-mechanistic models like classic Lotka-Volterra models already showed that coexistence in undisturbed habitats is possible only when intra-specific competition is stronger than inter-specific competition. With our simulations, we show a possible mechanism behind this principle of negative frequency dependence.

Not all types could coexist as a result of the negative frequency dependence that acted on plants that invested more in height growth. Only types with contrasting height growth (one with lower and one with higher than the optimal intermediate investment in height growth) could coexist. With types that had either extremely small or large investment in height growth, the range of types with which each of the types could coexist was broad. The whole range of height investment considered in this chapter was 0 to 50 % of net photosynthetic production. As an example, a type with small (2.5%) height growth investment could coexist with types that invested in height growth in a range of 40-50%. Similarly, a type with a large (47.5%) investment in height growth could coexist with types that invested in height growth in a range of 0-10%. Towards the mid-position of the range of height growth investment, the range in possibilities for coexistence became smaller (Figure 13). As discussed in Inouye & Schaffer (1981), the outcome of de Wit (1960) replacement series, used in this chapter for the investigation of the effect of frequency on coexistence possibilities, can be different depending on the densities. Although the pattern can shift, the general pattern of frequency dependent coexistence as depicted in Figure 13 will be similar with a change in density. At higher densities, plants with large height growth will be self-limiting at a lower frequency.

The distinct patterns of coexistence that were found between pairs of contrasting types have not been mentioned before in literature data as far as we know. It will have to be either confirmed or discarded with controlled experiments.

Appendix

Table 4. Parameters as used in the model. Sources of the parameters: 1. Poorter (1991) 2. Goudriaan & Van Laar (1994) 3. Anten (1996) 4. Calibrated parameters (this study). For an overview of parameters, see Appendix 3 in Chapter 2.

Parameter	Value	Unit	Source
Initial leaf area	0.00165	m ²	1
Initial height	0.01	m	4
Gram leaf per m ² leaf	33.3	g/ m ²	1
Root / Leaf partitioning	0.5	g root/ g leaf	4
Stem shape parameters α , β	0.018, 1.4	-	4
Volume per gram stem	0.0001	m ³ / g stem	4
Shape parameters p_0, p_1, p_2	30, 2.0, 2.0	-	4
Carbon per gram mass	0.45	g C/ g mass	2
Photon flux density	1700	$\mu\text{mol photons/ m}^2/ \text{s}$	3
Seconds of light per day	25200	s/ day	4
Leaf photosynthetic capacity	16	$\mu\text{mol CO}_2/ \text{m}^2/ \text{s}$	3
Leaf Angle α	0.5	Degree from horizontal	2
Phi Φ	0.05	$\mu\text{mol CO}_2/ \mu\text{mol photons}$	3
Curvature θ	0.7	-	3
Growth respiration	0.213	g C/ g C mass	2
Maintenance constant	0.0235	g C/ g C mass/ day	2
Seed allocation	0.5	g C/ g C npp	4
Leaf + root retractable C	0.6	g C/ g C mass	4
Surface of ground area	0.001	m ²	4

Table 5. Characteristics of plants as resulting from initial parameter settings.

Characteristic	Value	Unit
Total initial plant weight	0.1	g
Initial leaf mass	0.055	g
Initial root mass	0.027	g
Initial stem mass	0.018	g
Leaf area ratio	0.00165	m ² /g plant
Shoot / root ratio	2.7	g/ g

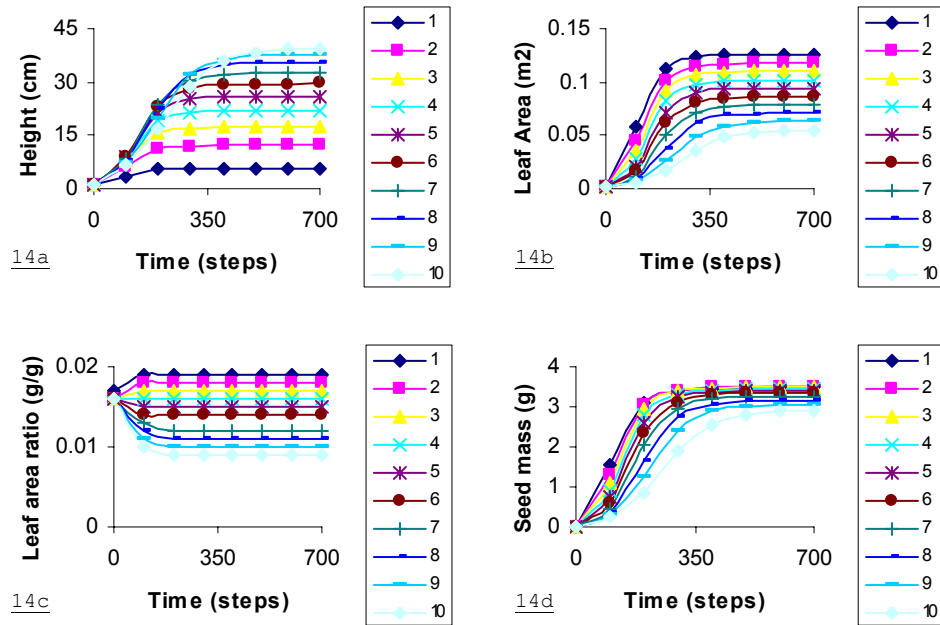


Figure 14. Simulated growth of single isolated plants during 700 timesteps. (a) Height development (b) Leaf area development (c) Leaf area ratio (d) Seed mass production. The figures show the growth of height growth types 1 to 10. For a description of types see Table 1.

PLANT GAMES WITH HEIGHT

Summary

Using game theory, we explored the possibilities for coexistence of plant types that differ in the proportion of net photosynthetic production allocated to height growth. Plant types could be plastic or rigid in the investment in height. It was found that, in a simulated vegetation, extinction times varied for plant types. Eventually however, only one type with medium height investment survived in all simulations. Plants with a late investment in height outcompeted plants with an early investment in height, in most combinations of types. The distribution of leaves along the height of a plant had a substantial influence on plant performance. Plants with an extremely high positioned leaf area performed badly in combination with a large height growth investment. Shortening the season length was beneficial for plants with a low investment in height and led to general longer extinction times of plants. Increasing the density caused a better performance of plants with larger investment in height. In none of the performed analysis an evolutionary stable coexistence between two or more types was found. Only when explicit space was considered, several types of various height investments could coexist. This was brought about by the stochastic differences in plant density between patches. Coexistence between plants of different stature, as often observed in nature, could not be explained by their different height growth patterns *per se*. (Random-) variation in densities however did provide conditions for types of various height growth strategies to coexist.

Keywords: game theory, height growth, plasticity diversity, mechanistic model, plant traits, ontogenetic investment

Introduction

In herbaceous vegetations, individuals of annual plant types differ in their spatial position from year to year because of death and dispersal processes (Otsus & Zobel, 2002). In such stands, the individuals of a particular plant type may have to compete with many other plant types that possess different trait values. From the standpoint of Darwinian fitness, the individuals of a plant type possessing a successful trait must not only be well adapted to the a-biotic environment but also adaptive with respect to potential competition with other plants. In this view, the success of the plant type depends on the characteristics and frequencies of neighbouring plants (Riechert & Hammerstein, 1983).

In this kind of competitive setting, game theory is a necessary tool to analyse the Darwinian fitness of individuals possessing different traits. This is especially true when analysing the fitness value of a trait such as height (Westoby et al., 2002) and the height of leaf area (Givnish, 1982). A tall stature is advantageous because it enables plants to capture light that would otherwise come available to neighbours. The adaptive value of height will become apparent in the competition with neighbouring plants and can therefore only be understood in a competitive context (Iwasa et al., 1984; Westoby et al., 2002). However, plant height at any point in time incurs costs from former investments in stem tissue, support structures and maintenance costs (Westoby et al., 2002). Also, investments in height result in a reduced investment in resource harvesting plant organs such as leaf area and roots. This will have to be taken into account to fully appreciate the role of height for the success of plants.

Several studies have investigated the role of height investment on coexistence of plants. Hirose & Werger (1995) and Anten & Hirose (1999) showed that short and tall plants could achieve similar light harvesting efficiencies per unit biomass. This could facilitate coexistence. Under the assumption of completely one-sided competition, Iwasa et al. (1984) and also Perry et al. (2003) found that if the thickness of crowns was thin enough, an infinite number of plants with non-overlapping crowns and differing in height could coexist. In a similar study, Huisman et al. (1999) found that a tall and subordinate species could stably coexist. All these analysis however (except for the study of Perry et al., 2003) are only valid for static, non-growing plants. Anten & Hirose (1999) already showed that the light harvesting efficiencies for plants of different heights are not static but vary over the course of a season. Yokozawa et al. (1996), investigating coexistence during one generation of dynamically competing plant types, showed that initial height affected the survival time of species in competition when comparing model trees with spherical and conical crowns.

In their review on plant height and evolutionary games, Falster & Westoby (2003) found that most game theoretical modelling studies on this subject (except for the static model of Iwasa et al., 1984) found monomorphic equilibria, meaning that only one type was evolutionary stable. Game theoretic modelling has been used not only to analyse possibilities for coexistence but also to predict trends in the development of certain traits as a function of frequency and density of other phenotypes (Givnish, 1982). With respect to height growth, Givnish (1982) found that herbs in densely populated environments had

a higher evolutionary stable leaf height than herbs in scarcely populated environments. King (1990) found that trees under the influence of competition for light attained a height some proportion of the maximum possible height and should cease height growth abruptly when reaching this height. Iwasa et al. (1984) found that height increased with tree density and amount of leaves per tree, but decreased with crown thickness. All these studies assumed either a simple function with linear trade-offs to describe plant growth, or a static model for their game theoretic calculations. Investigations of this kind will fail to capture the broad spectrum of possible plant behaviours. This will only be achieved by applying game theoretic modelling that is based on a more mechanistic and dynamic plant growth model.

In this chapter, we analyse the evolutionary stable strategy (ESS) in height investment, with the help of game theoretic modelling. The bases of the calculations are the results of a mechanistic plant growth model. We will also study the influence of the length of the growing season, the influence of leaf area distribution over height, the timing of height investment and the influence of density on the time-course and outcome of competition. The ultimate objective is to see whether a polymorphic equilibrium is possible for types that possess different height allocation strategies.

Methods

The calculations in this chapter are done with a mechanistic competition model that is developed in Chapter 2. As a measure of fitness, the model calculates lifetime storage of carbon. It is assumed that this carbon is used for the production of seed. Calculations are done for pairs of plants that are competing for light. In Chapter 3, growth and fitness of pair-wise competing plants with different height investment strategies were analysed. In this chapter, we apply a game theoretic approach to explore the possibilities of coexistence between these different plant types. We will start with analysing plants that invest a constant portion of their net photosynthetic production in height growth. We call this the rigid height investment (RHI) strategy. We distinguish 10 types that invest different fixed fractions of net photosynthetic production in height growth (see Table 1).

Table 1. Constant percentage of net photosynthetic production invested in height growth for all distinguished types of the RHI strategy. For an explanation of the differences in height investment values between RHI types, we refer to Chapter 3.

RHI type	1	2	3	4	5	6	7	8	9	10
Investment in height (%)	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5

In the simulations on frequency dependent competition between pairs of types in Chapter 3, it was found that contrasting types of the RHI strategy could coexist. We now explore whether coexistence is possible when we allow more types to compete within one arena. To evaluate the performance of types when influenced by many other types, we perform the following calculations. For simplicity, again we allow only pair-wise interactions between plant types. For every possible combination of competing pairs of types, we take per plant the total stored carbon (for the production of seed mass) as a measure of fitness. The model is run for a simulation period of 700 time steps, in which all plants are able to reach steady state. Steady state is the point at which the cost from maintenance of plants mass equals the income from gross photosynthetic production. Net photosynthesis is zero and no growth can occur any longer. All plants die at the end of each simulation period. At this time, we evaluate the amount of stored carbon for seed, as this is the measure of fitness. The fitness of a type in a particular combination is called ‘pay-off’ for the type in that combination. Every pay-off of a type in combination with another type is put into a ‘pay-off matrix’ (Riechert & Hammerstein ,1983). The matrix is constructed as follows:

$$\text{Pay-off Matrix} \quad \begin{bmatrix} p_{ij} & \cdot & \cdot & \cdot & p_{in} \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ p_{nj} & \cdot & \cdot & \cdot & p_{nm} \end{bmatrix} \quad (4.1)$$

Here p_{ij} is the pay-off of a plant type i competing against plant type j . In total, there are n plant types. From this pay-off matrix, we can calculate the development of the frequency of types over subsequent years.

We assume a field of plants, in which types are initially present at equal frequency. The total pay-off during one single simulation period (e.g. one growing season) of a particular plant type present in this field will depend on the chance of an encounter with the various other plant types present. The chance of encountering a type is dependent on the frequency of the type in the field (Mahdi & Law, 1987). This is under the assumption that all plants are randomly distributed over an infinitely large area. The success of a plant does not only depend on its competitive vigour in combination with every other plant type, but also on the frequency of the encounters with every plant type. The final pay-off is the combined effect of all pair-wise contests with plant types present in the vegetation. The total seed production of a plant type is the population size of that type in the next year. The plant type for which we calculate the total seed output is called ‘target’, whereas the plant type it competes with is called ‘opponent’.

The average total pay-off ‘ P ’ for a plant type i that is present at frequency f_i , is calculated as the summed total of the plant type’s seed output when competing with all other possible opponent types j , which are present at different frequencies f_j .

$$\text{Pay-off of target plant type } i \quad P_i = f_i \cdot \sum (p_{ij} \cdot f_j) \quad (4.2)$$

Now the frequency of target plant types in the next generation can be calculated. It is the relative contribution from the current pay-off of the target plant to the current total combined pay-off of all competing plants.

$$\text{New Frequency of target plant type} \quad f_{it+1} = \frac{P_{it}}{\sum P_{jt}} \quad (4.3)$$

With each repeated calculation, the frequencies of plant types in the community will change in the manner described above. The pay-off of a type will change with the composition of the plant stand. When the frequency of a plant type drops below a certain threshold frequency, the type is supposed to be extinct and its frequency is set to zero. The threshold frequency is set to 1 in 100.000. If there is no change in the frequencies of all participating plant types, equilibrium is reached. In that situation different plant types coexist, each one with its own frequency, or there is no coexistence and only one plant type perseveres.

Results

Rigid height investment plants

Listed in Table 2 is the pay-off matrix of rigid height investment (RHI) strategy types. In the matrix are the simulated seed masses for target plant types in every pair-wise combination of competing types.

Table 2. Seed output (gram per plant) of RHI target plant types in pair-wise competition with RHI opponent plant types. For a description of types, see Table 1. The highest seed output of a target type against a particular opponent type is written bold.

Opponent	Target plant types									
	1	2	3	4	5	6	7	8	9	10
Type 1	1.67	3.52	3.49	3.45	3.40	3.34	3.26	3.17	3.06	2.90
Type 2	0.70	1.72	3.49	3.45	3.40	3.34	3.26	0.38	0.27	0.20
Type 3	0.78	0.92	1.72	3.45	3.40	0.66	0.45	0.33	0.25	0.20
Type 4	0.92	1.02	1.23	1.70	1.00	0.68	0.48	0.36	0.27	0.21
Type 5	1.09	1.22	1.62	3.45	1.68	0.84	0.58	0.42	0.31	0.23
Type 6	1.29	1.53	3.49	3.45	3.40	1.65	0.77	0.52	0.37	0.27
Type 7	1.52	2.13	3.49	3.45	3.40	3.34	1.61	0.72	0.47	0.33
Type 8	1.78	3.52	3.49	3.45	3.40	3.34	3.26	1.57	0.67	0.43
Type 9	2.08	3.52	3.49	3.45	3.40	3.34	3.26	3.17	1.52	0.61
Type 10	2.41	3.52	3.49	3.45	3.40	3.34	3.26	3.17	3.06	1.44

Given in the columns of Table 2 are the performances of a single target plant types in competition with different opponents. The rows of Table 2 show the performances of different target types against opponents of a single type.

To evaluate if one RHI type is better than all other types or if the success of a plant type depends on the type of opponent, we look at the rows of Table 2. Against an opponent of type 1, target plant type 2 has the highest seed output. Against an opponent of type 2, however, target plant type 3 has the highest seed output. When this analysis is continued, it is clear that the best performing type depends on the kind of opponent type. In other words, it will depend on the composition of types in the field what type performs best.

If we let the plants play in a field with a particular composition of types, the type that has the best average performance against all types present will produce the highest seed mass. Types that, on average, perform badly against all types will produce a very low seed mass. Because it is assumed that the seed mass will constitute the population size of the types in the next generation, the types will increase or decrease in frequency accordingly. In Table 3 is the total seed output per target type when competing against all opponent types, in the case when all types are equally abundant. This will be the starting condition for the game-dynamic calculations.

Table 3. Total seed output per RHI type at equal abundance. Seed output is summed over all combinations with opponent types. For seed output per combination, see Table 2. For a description of types, see Table 1.

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7	Type 8	Type 9	Type 10
Seed mass	14.23	22.61	29.01	32.74	29.85	23.84	20.21	13.81	10.24	6.82

In relation to Table 2, the total seed output per target type is the sum of the seed outputs in a column. RHI strategy type 4 has the best performance when all types are equally abundant (Table 3).

The question is how the composition of the field will change with repeated calculations. We explore this question using the formulas 4.2 and 4.3, as explained in the previous section. The pay-offs in Table 2 are the basis for the game-dynamic calculations. In Figure 1, the calculated frequencies of the plant types are plotted for 30 growing seasons (these are equivalent to years).

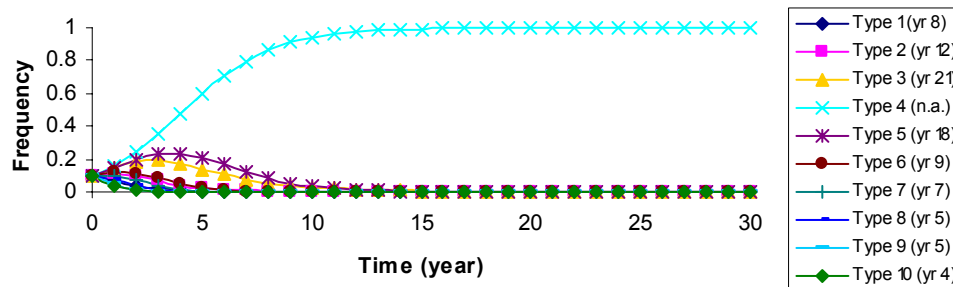


Figure 1. Frequency developments of competing types of the RHI strategy. Exact extinction times of the different types are depicted in the legend. For a description of types, see Table 1.

Apparently, only one RHI type (type 4) perseveres eventually. The extreme high and low RHI types go extinct fastest. This is because these types with high and low height investments perform poorly against nearly all other types. At each calculation, the plant with the highest average pay-off over the field increases in frequency. Type 4 has the highest average pay-off already from the start of the calculations (see Table 3) and continues to have the highest pay-off whether extreme types are present or extinct (Figure 1). It can therefore be concluded that, in this particular case, it is of no consequence that the poor performers go extinct. In whichever remaining combination, type 4 performs best on average and increases in frequency.

To understand why exactly type 4 wins the competition, we briefly repeat the underlying mechanisms why medium RHI types perform better than other types. Medium RHI types do not have very large costs of stem investment and can therefore make a relatively large leaf area. They can overshadow low RHI types at an early stage. On the other hand, they interfere with higher RHI types, which need to intercept a lot of light to account for the costs of their larger height growth. Because of the interference, the high RHI types cannot make a large leaf area and hence do not severely overshadow the medium RHI types. Consequently, medium RHI types can perform well. For a more elaborate explanation, see Chapter 3.

The effect of the length of the season

Up to now, simulations are carried out until all plants have reached steady state. This point is reached usually after a simulation period of 700 time steps. In a field situation, one will rarely encounter plants in steady state. It is therefore of interest to study the effects of differences in the length of the season on the outcome of competition. Accordingly, we analyse the state of RHI plant types after 150 time steps. This is the point when, in our simulations, all types usually reach their maximal relative growth rate.

For this analysis, we do not show the pay-off matrix. When we apply game-dynamic calculations, RHI type 3 wins (Figure 2). This type invests less in height compared to the winner of the 700-time step season simulation, which was RHI type 4 (Figure 1). The explanation for this result lies in the fact that, earlier in competition, the high RHI types lag behind in growth and performance due to a small leaf area. The lower height investment types make use of the early part of the growing season. They have a large leaf area and are not yet severely overshadowed. Consequently, they have a higher fitness relative to higher height investment types at this stage.

Another difference between the simulations with 150 or 700 time steps is that the extinction time of all plant types is longer. Some plant types can even coexist during the whole simulation period of 30 years. This is because the differences in seed production in a simulation period of 150 time steps are not so profound as with a simulation of 700 time steps. The shorter the time span in which the plants are allowed to grow, the less profound the differences in performance between competing species can get. Selection therefore works less severe. Eventually, however, again only one type is left and no coexistence occurs.

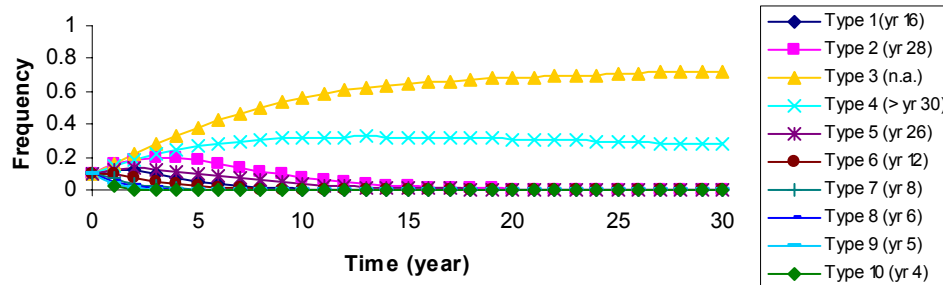


Figure 2. Frequency development of pay-off matrix of RHI types, with a growing season of 150 time steps. Time-scale in years. Exact extinction times are depicted in the legend. For a description of types, see Table 1.

Other simulations (not shown here) in addition to the simulation above, show that the qualitative pattern of plant performances as observed in Table 2 does not change. However, the shorter the length of the season is taken, the lower the ESS types. The ESS height investment thus shows a consistent and predictable reaction to the season length.

The effect of density

So far, all plant types have competed at a density of 200 plants per square meter. We now investigate what happens if we increase the density quite rigorously to 800 plants per square meter. Competition is again assumed to be pair-wise. For this analysis, we do not

show the pay-off matrix. The extinction times of the different plant types are in the legend of Figure 3.

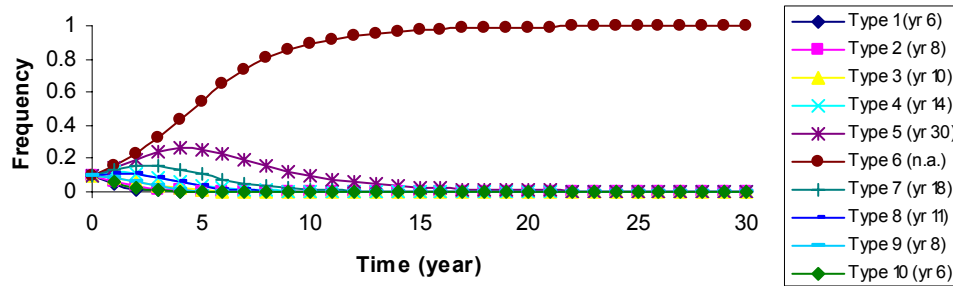


Figure 3. Frequency development of RHI types at a density of 800 plants per square meter. Extinction times of different types are in the legend. For a description of types, see Table 1.

In this dense stand, RHI type 6 is the optimal type (see Figure 3). In the previous simulations, with the standard stand density, RHI type 4 performed best. When we further increase the density, a type with an even higher investment will win (data not shown). This is again a consistent and predictable pattern. It seems that in a denser stand, a higher height investment gives a better performance. High densities have a negative effect especially on the performance of low investment RHI types.

When density of plants is increased, the shading increases. The average light available per plant is very low. Extra leaf area will not intercept a lot of extra light. Increasing in height will be much more advantageous because it gives a disproportionate advantage in light interception. As higher investment RHI types become more abundant, the environment becomes even more unfavourable. Although costs for height growth are considerable because of carbon investments in the stem part, it pays to grow in height to escape the poor light climate. In short, plants need to ‘shade or be over shaded’. Besides the overshadowing of subordinate plants, there is an intrinsic advantage to be tall in dense stands. A population of tall plants performs better than a population of smaller plants. This is because an increase in height investment is accompanied by a reduction in leaf area investment. In a population with individuals with a small leaf area, shading is not so severe. Consequently, more individuals can persevere and produce seed. With increasing density, the seed output per individual decreases but the seed output as a population is higher. Only at very high densities, the population collapses.

The effect of leaf area distribution over height

So far, we have considered plants with their leaf area distributed vertically symmetric. The positioning of leaves in the light gradient is very important for the light acquisition of competing plants. Therefore, we will now analyse the success of types that have their leaf area more towards the top of the plant ('high bulk') or towards the bottom ('low bulk'). High bulk plants will be at an advantage because their leaves are at a higher position than low bulk plants. No extra costs are assumed with having the leaves at a high position. Although it seems intuitively clear that high bulk plants should win competition when competing with low bulk plants, there are some unexpected results.

Almost in every combination, high bulk types have a higher seed production than low bulk plants. Nevertheless, with a high investment in height, the high bulk plants perform less and are influenced by the type of competitor. When the high bulk plant has a very high height investment, it even performs worse than a low bulk plant. In short, it easily pays to have the bulk high, but having the bulk too high will reduce the benefits for the plant, especially when it is accompanied with large height investment. The explanation of these results lies in the reallocation of leaf area with height growth. When our plants grow in height, they make new leaves at the top of the stem and drop leaves at the underside, as imposed by the used leaf area distribution formula. The higher the bulk is situated on a plant, the more leaf area will have to be relocated with a given growth in height (see Figure 4). In addition, the more a high bulk plant invests in height growth, the higher the costs of the leaf area reallocation. This imposes extra costs on the plant. The plant has less carbon to invest in leaf area and hence the seed production is lower. Plants that have the bulk of their leaf area low have less costs of leaf area reallocation with height growth because they have less area to relocate (compare Figure 4a and b). Because they do not have large costs for leaf relocation, the low-bulk plants can invest the surplus of net photosynthesis production in extra leaf area.

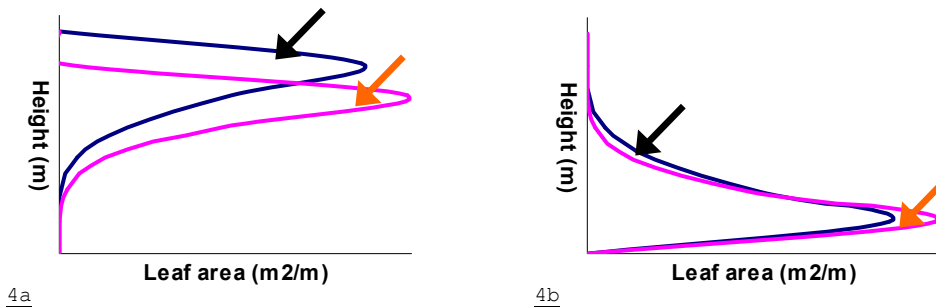


Figure 4. Leaf area relocation for a high (a) and a low-bulk plant (b) with a height increment of 15%. The light line depicts the old shape, the dark line depicts the new shape after the height increment. Dark arrows depict the leaf area that is newly produced. Light arrows depict the leaf area that is shed. Both plants in (a) and (b) are similar with respect to total height and leaf area.

The type that wins in game-dynamic calculations is the high bulk plant RHI type 3. This type is superior throughout the whole simulation. In simulations on neutral bulk types, height growth type 4 was superior. Because a high bulk is unbeneficial in combination with height growth, a lower height growth type now is the ESS.

Plastic height investment plant types

The second strategy we consider in this chapter is the plastic height investment (PHI) strategy. Plants of this strategy invest in height growth based on a shading signal. For a description of the shading signal, see Section 5 of Chapter 2. The PHI types invest a maximum of 2.5% to 70% of net carbon production in height. The types differ in steps of 7.5% of maximal investment in height growth. See Table 4 for an overview of types within the PHI strategy. In plants of the PHI strategy, there can be a difference between maximal and realised height investment. With less than full shading, the plant invests only a part of the maximum investment of net photosynthetic production in height, in proportion to the amount of shading. The realised height investment is the actual investment in height under the current shading. Shade is brought about either by neighbouring plants or by self-shading. Because shade is rarely one hundred percent, the realised height investment usually is less than the maximal height investment.

Table 4. Maximum attainable percentage of net photosynthetic production invested in height growth for all distinguished types of the PHI strategy.

PHI type	1	2	3	4	5	6	7	8	9	10
maximal investment in height (%)	2.5	10	17.5	25	32.5	40	47.5	55	62.5	70

PHI types initially will not be subjected to severe shading because plants start with a small leaf area (see Chapter 3). Consequently, PHI types initially invest only little carbon from net photosynthetic production in height and a lot in leaf area. In contrast to the RHI strategy plants, PHI strategy plants have to ‘wait’ until they are shaded before they can grow in height. A possible advantage of PHI strategy plants is that they will decrease their height investment if they have reached a better light climate and thus omit unnecessary costs for height growth.

As a consequence of the response to the environment of PHI types, the dynamic pattern of height investment differs between PHI and RHI strategy plants. For this reason it is difficult to compare types within the Rigid and Plastic height investment strategies. The actual height investment at any point in time is not very informative for it does not reflect the total lifetime investment in height. It is possible to adjust the functional response to shade for PHI plants (see Formula 5.6 in Chapter 2). This can be fine tuned

until the total lifetime height investment of rigid- and plastic height investment types is comparable. The resulting attained height, height drive, leaf area and seed mass after 700 simulation steps are compared between RHI and PHI type plants in Figure 5.

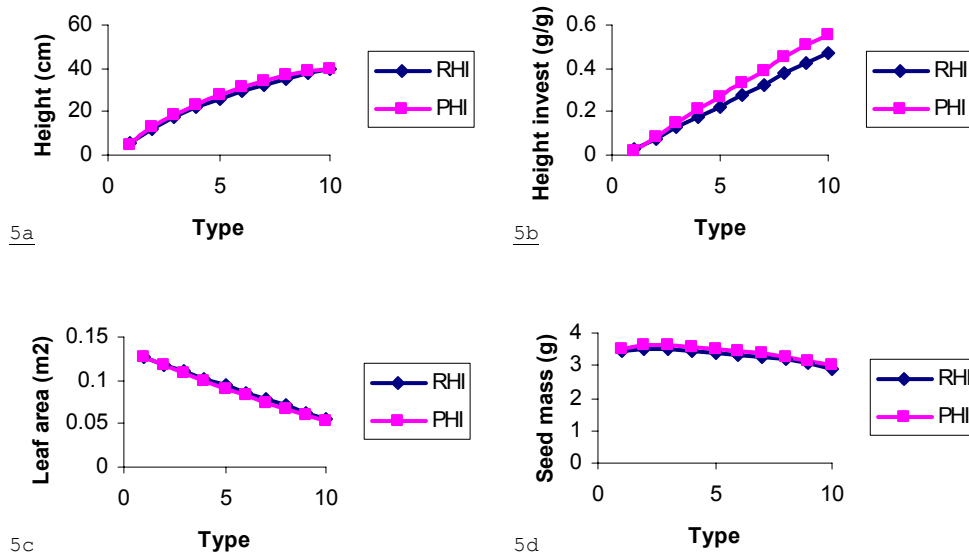


Figure 5. Comparing performance of single, isolated PHI and RHI types after 700 simulation steps. Attained height (a), final height investment (b), Leaf area (c), Seed mass production (d). For a description of types, see Table 1 and Table 4.

Figure 5 shows that after tuning the response of the PHI plants on shade, the final attained shape and fitness is comparable between single isolated Rigid and Plastic height investment types. Logically, the final height drive is larger for PHI types. Given the fact that PHI types will initially invest little in height growth, the end investment towards the end of growth has to be bigger to achieve a similar height as RHI types.

Mixed height investment strategies: Rigid versus Plastic height investment

In the previous paragraphs, we have discussed the behaviour of PHI and RHI strategy types. The performance of types of both strategies was very comparable. Nevertheless, there is a difference in the timing of height investment in both strategies. PHI types can only react to the environment they experience whereas RHI types invest in height from the start of growth. Types of the latter strategy may gain a head start, consequently shading the PHI plant types. Many studies find that an early quick height growth (in the seedling stage) will give plants a competitive advantage (Ballare 1990; Miller, 1995; Maloof et al., 2000; Weinig, 2000b). Nevertheless, a plant that invests in height based on

light availability will possibly show the appropriate height investment in more situations. Below, we will address the question which of the PHI or RHI strategies is better under which circumstances.

Table 5 presents the pay-off of RHI target plant types in pair-wise competition with PHI opponents. Table 6 presents the pay-off of PHI target plant types in pair-wise competition with RHI opponents.

Table 5. Seed output (gram per plant) of RHI target plant types in pair-wise competition with PHI opponent plant types. The highest seed output of a target type against a particular opponent type is written bold. For a description of types, see Table 1 and Table 4.

PHI Opponent	RHI Target plant types									
	1	2	3	4	5	6	7	8	9	10
Type 1	3.48	3.52	3.49	3.45	3.40	3.34	3.26	3.17	3.06	2.90
Type 2	0.68	3.52	3.49	3.45	3.40	3.34	3.26	0.38	0.27	0.20
Type 3	0.70	0.84	1.03	1.12	0.81	0.57	0.41	0.31	0.24	0.19
Type 4	0.77	0.85	0.91	0.87	0.71	0.54	0.41	0.31	0.24	0.19
Type 5	0.85	0.92	0.97	0.92	0.75	0.58	0.43	0.33	0.25	0.20
Type 6	0.94	1.02	1.09	1.05	0.87	0.65	0.48	0.36	0.27	0.21
Type 7	1.04	1.15	1.28	1.28	1.06	0.78	0.56	0.41	0.30	0.23
Type 8	1.15	1.31	1.57	3.45	1.51	1.00	0.68	0.47	0.34	0.25
Type 9	1.27	1.51	3.49	3.45	3.40	3.33	0.88	0.57	0.39	0.28
Type 10	1.39	1.75	3.49	3.45	3.40	3.34	3.23	0.74	0.47	0.32

Table 6. Seed output (gram per plant) of PHI target plant types in pair-wise competition with RHI opponent plant types. The highest seed output of a target type against a particular opponent type is written bold. For a description of types, see Table 1 and Table 4.

RHI Opponent	PHI Target plant types									
	1	2	3	4	5	6	7	8	9	10
Type 1	0.79	3.60	3.58	3.54	3.49	3.42	3.34	3.24	3.12	2.97
Type 2	0.68	1.29	3.56	3.52	3.46	3.40	3.31	3.21	3.08	2.90
Type 3	0.78	0.95	3.55	3.51	3.45	3.38	3.29	3.18	0.87	0.60
Type 4	0.92	1.06	3.55	3.51	3.45	3.38	3.29	1.14	0.73	0.58
Type 5	1.09	1.26	3.56	3.51	3.45	3.38	3.29	3.17	0.85	0.66
Type 6	1.29	1.58	3.56	3.52	3.46	3.39	3.30	3.19	1.31	0.83
Type 7	1.51	2.25	3.57	3.52	3.46	3.39	3.31	3.20	3.07	1.49
Type 8	1.76	3.60	3.57	3.53	3.47	3.40	3.32	3.22	3.09	2.92
Type 9	2.04	3.60	3.58	3.53	3.47	3.41	3.32	3.22	3.10	2.94
Type 10	2.33	3.60	3.58	3.54	3.48	3.41	3.33	3.23	3.11	2.96

In Tables 5 and 6, the type with the best performance against an opponent type is written bold. Both tables show that it depends on the opponent type, which target type performs best. To evaluate in what circumstances a RHI strategy is better than a PHI strategy, the seed output per combination of RHI types (in Table 5) and PHI types (in Table 6) have to be compared. For example, in the combination of RHI type 1 and PHI type 1, the RHI type has a seed output of 3.48 (Table 5) whereas in this combination PHI type has a seed output of 0.79 (Table 6). The RHI type performs better than the PHI type in this case. In most combinations, however, PHI types are better. RHI strategy plants are better only in the combination of low investment RHI plants with low investment PHI plants. At combinations of higher height investment types, plants with a PHI strategy have a higher seed output than RHI strategy plants. The reason behind the superiority of high investment PHI types is in their ability to adjust their height growth. The initial height growth is small because shading is not severe. This proves an advantage because all surplus carbon can be invested in leaves. Nevertheless, the potential for height growth is present, and as soon as it is triggered by shadow, the plants can grow in height, powered by their big leaf area and consequent light interception. The reason that RHI types can not benefit from their larger initial height is because the larger height growth is accompanied by a small leaf area growth. Consequently, the plants do not severely inhibit the growth of plants of smaller stature. RHI types with a lower height investment do produce a large leaf area and they can benefit from the initial overtopping of PHI types.

For the game-dynamic calculations, we again assume a field of pair-wise competing plants. In this field, the types of either strategy can encounter types of con-specifics or hetero-specifics. For this reason, aside from the pay-off in Table 5 and 6, the pay-off of rigid plants competing with rigid plants (in Table 2) and from plastic plants competing with plastic plants (not shown, but this can be compared to the pattern as in Table 2) have to be included in the calculations. In Table 7 is the summed pay-off of target types of both strategies, competing with hetero-specific types and con-specific types respectively.

Table 7. Total seed output per strategy type, summed over all combinations with hetero-specific or con-specific opponents respectively. All types are assumed equally frequent. For a description of types, see Table 1 and Table 4.

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7	Type 8	Type 9	Type 10
PHI (RHI opponents)	13.2	22.8	35.7	35.2	34.6	34.0	33.1	30.0	22.3	18.9
PHI (PHI opponents)	11.3	19.5	26.8	31.2	34.5	31.7	26.3	23.2	21.2	15.6
RHI (PHI opponents)	12.3	16.4	20.8	22.5	19.3	17.5	13.6	7.0	5.8	5.0
RHI (RHI opponents)	14.2	22.6	29.0	32.7	29.9	23.8	20.2	13.8	10.2	6.8

Depicted in Figure 6 are the frequency developments and the extinction times of the different competing types.

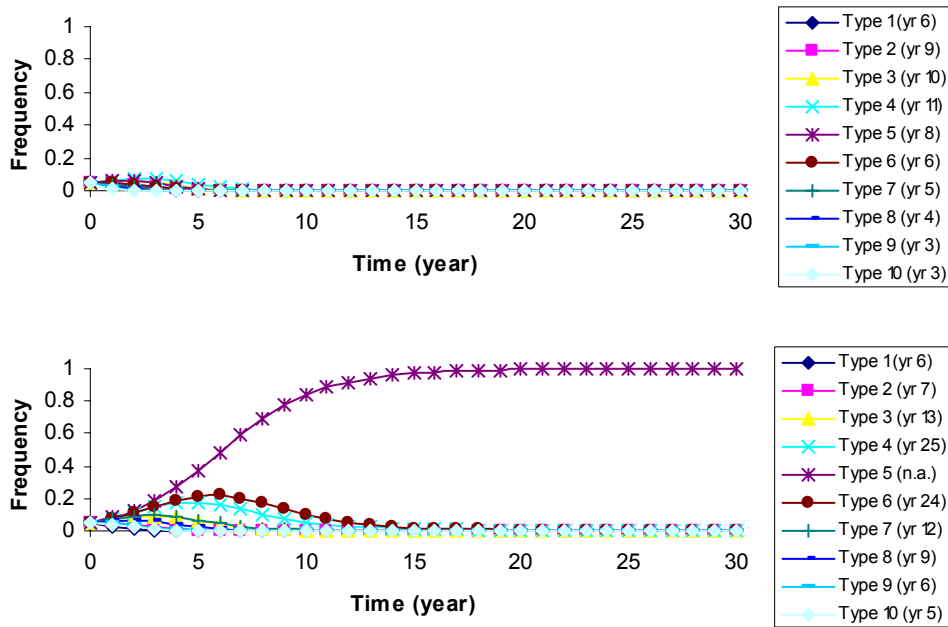


Figure 6. Frequency developments for competing RHI (top figure) and PHI (lower figure) strategy types. The extinction times of the types are in the legend. For a description of types, see Table 1 and Table 4.

In the game-dynamic calculations on competing PHI and RHI types, PHI type 5 wins after 30 years of simulation. The legend of the top graph shows that all RHI types go extinct quickly. No coexistence is found between or within types of both strategies.

To summarise, the advantage that PHI strategy types have over RHI strategy types is that they develop a big leaf area early in the simulation in combination with a potential to grow in height. It seems that a large leaf area early in competition, followed by a larger maximum plant height, is important for the competitive vigour of plant types. The same result was found in a model study of Bastiaans et al. (1997). If we increase the initial leaf area per plant for both types, RHI types get a more profound head start. RHI types then win in more cases, and loose only if they have a low height investment and compete with high investment PHI plants. A PHI type however continues to perform best in game-dynamic calculations.

Density dependent processes in an explicit space

Until this point, we have kept the density per simulation constant. The influence of density was investigated in a previous section. With an increasing density, a type with more height investment was evolutionary stable. The question can be posed to what density the community will develop if density is not held constant. If we want to include dynamically varying densities, we will have to include explicit seeds. We will also relax the mean-field assumption, by introducing explicit space. In previous sections, we saw that the qualitative behaviour did not differ between PHI and RHI plants. For clarity, we show the analysis only for RHI type plants. For PHI type plants, a similar result was found, but this is not shown.

The environment in which plants grow consists of 40 by 40 vegetation cells. Each vegetation cell is 10 by 10 centimetres. The environment is initialised randomly with a low density of plants from every RHI type. From the stored carbohydrates per plant, it is calculated how many seeds can be formed. It is assumed that every seed has a weight of 0.2 grams. Seeds of successive years are distributed in the environment. The average density per cell in every year will depend on the total amount of seed produced by all individuals in the preceding year. By chance, some cells will have a higher abundance than average and others a lower abundance. In addition, the composition of types within a cell can differ. All seeds are assumed to germinate and grow. The performance of plants, however, will depend on the density and type of neighbours within the cell. We simulate the development of the different types in the environment for 30 years. The density development of the different RHI types is depicted in Figure 7.

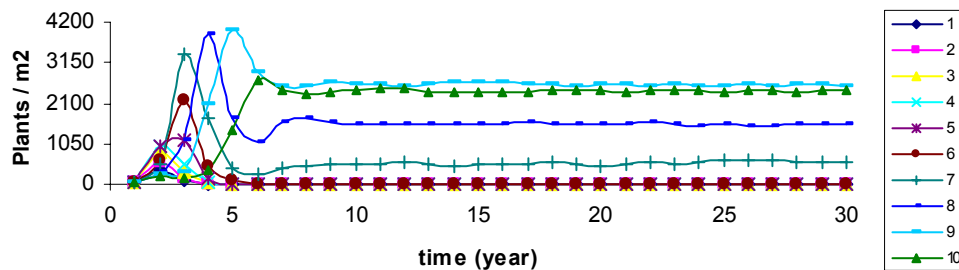


Figure 7. Density development of different RHI types in an explicit area of 40 by 40 cells, each of 10 by 10 cm. The area thus represents a total of 16 square meters. The distribution of seeds in the area between years is random. For an explanation of types, see Table 1.

Figure 7 shows that the introduction of explicit space and density allows for four RHI types to coexist in a stable way. Initially, the environment has a very low density of

plants. As the density increases, types that invest more in height perform better. However, in contrast to the simulations on systems with constant density and no explicit space, this does not imply that all plants with lower height investment go extinct. The explanation for this result lies in the different plant densities in cells in the environment. With random distribution of individuals over the cells, not all cells are equally dense. Different types perform optimal at different densities. As a result of the different densities between cells, types can find a ‘window of opportunity’. See Figure 8 for the density distribution of the cells in the simulation area.

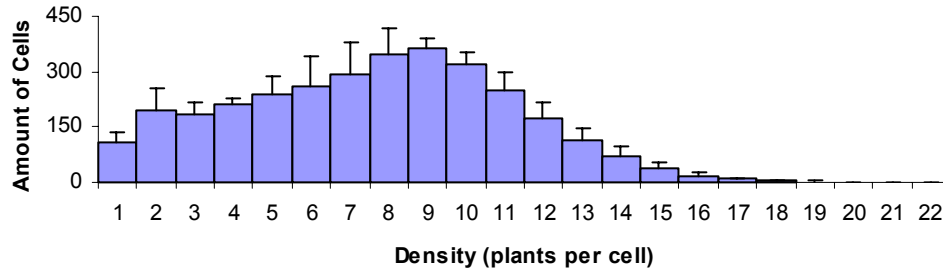


Figure 8. Density distribution at equilibrium in an area of 40 by 40 cells with randomly dispersing seeds (average of 4 years). For the composition and number of species in the area, see densities at equilibrium in Figure 7.

If a cell contains two plants, this coincides with a density of 200 plants per m^2 as the cells are 10 by 10 cm. In previous simulations, it was found that height investment type 4 was the optimal type at this density. At a density of eight plants per cell (800 plants per m^2) it was found that type 6 was optimal. The fact that these types do go extinct is caused by the relative importance of winning competition at low or high densities. At low densities, all individuals in a cell will be able to store some carbon for seed production. At high densities, competition is much more asymmetric and only the optimal type will be able to store enough carbon to produce seed. It is thus relatively more important to perform well at high densities, as the winning height investment types 10, 9, 8 and 7 do (see figure 7).

The RHI types currently differ 5 % in height investment. When the types would differ less in height investment, more types can coexist. It will depend on the density distribution, how many and which types can coexist. This is an example of coexistence by means of a transitive dominance, caused in this case by environmental differences (see Aarssen (1992) for a discussion on this subject).

Interestingly, the height distribution at steady state resembles a realistic distribution. Most plants are of a low stature, but there are two distinct layers of plants above it at approximately 22 cm and 35 cm (see Figure 9).

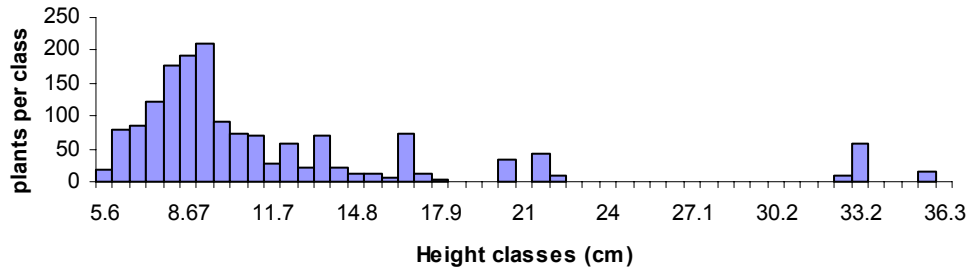


Figure 9. Height distribution of competing RHI types in a spatially explicit arena, at equilibrium. See Figure 7 for the population development of the RHI types. For a description of types, see table 2.

Short turf grassland canopies usually are stratified in two or more layers (Mitchley, 1988; Liira & Zobel, 2000). However, if a closer look is taken at the model results, it can be noticed that the different layers of the model vegetation do not represent different types of plants, as is the case in actual vegetation (Mitchley, 1988). In the model vegetation, each type attained several distinct heights, rather than each type occupying a specific layer. The cause lies in the different circumstances for plants in the vegetation cells. Even if a type is superior at some density and can grow to a certain height, in another cell it can be subordinate and stay lower. This demonstrates once again that it is important to be aware of the mechanisms behind a pattern, before conclusions are drawn with regard to the real field situation.

Discussion

We found no long-term stable coexistence among any of the plant types differing in height growth. The analyses were done within a game theoretic framework, in which frequency dependent interactions were taken into account. After a number of years, one type within a strategy became the winning type and excluded all other types. The environment precluded both extreme investments in height and in leaf area, leaving a medium type evolutionary stable. Iwasa et al. (1984) found polymorphic equilibria of plants differing in height using his model. Falster & Westoby (2003) suggest that the study of Iwasa et al. (1984) is likely the most promising basis for future work. They largely base their assessment on the notion that this model predicts multiple coexisting strategies, as can be observed in nature. Nevertheless, a similarity between predicted and observed patterns does not confirm that a model accurately mimics reality. Among other things, the polymorphic equilibrium in Iwasa's study is made possible by the assumption that tree crowns do not interfere with each other. In forests, or any other plant community, it is clear that there is some measure of mutual interference between plants of different

height, because of crown overlap (Yokozawa & Hara, 1992; Geritz, 1995; Hirose & Werger, 1995). In addition, the static nature of his study can be put to question, a notion that Falster & Westoby (2003) themselves also put forward. It is not only important to calculate that two species can coexist when they are evaluated at a certain shape, but one also has to take into account how these species could get to that size. The instantaneous benefits of traits do not take into account the costs that were made earlier on. Our study does take the whole dynamic process of growth into account. With an additional relaxing of the strictly one-sided interference, we found only monomorphic equilibria. Therefore, based on simulations of King (1990), Givnish (1982) and the present study, we cannot say that differences in height investment are a cause for an evolutionary stable coexistence of plant types.

In another simulation, we showed that the exact timing of carbon investment in height growth could give rise to differences in competitive ability. A change in phenotypic expression of traits caused by the environment is referred to as a plastic response (Scheiner, 1993). We distinguished plant types that invested in height growth on the basis of being shaded (plastic types) and plants that invested a constant proportion in height growth (rigid types). Both types possessed same underlying allocation trade-off between investment in height and leaf area. Only the timing of the investment was different. Plastic types delayed their height growth until shaded whereas rigid types invested in height growth right away. When rigid and plastic plants competed, the plastic plants performed relatively better. Because of the investment trade-off between leaf area and height, plastic types could initially invest more in leaf area. This enabled them to make a relatively large investment in height growth once they were shaded. Rigid plants invested in height right away and invested little in leaves, and the ability for light interception was therefore reduced. This hampered both competitiveness and growth. This result contradicts with earlier studies that conclude that early height growth should always be advantageous (Ballare et al., 1990; Miller, 1995; Weinig, 2000b). Early height growth might favour plants that are not able to overtop other plants in a later stage of development, but can gain an initial advantage by reacting quickly. One reason for the poor performance of the immediate (and thus early) height growth types in our simulation could be that they continuously invest in height. In real plants, a reduction of height growth occurs after an initial investment in height (Maloof et al., 2000). This reduction of height growth might be needed to limit the costs of height investment and in this way allow a plant to invest in leaves as well. Height growth at a later stage of development, as occurred in our plastic types, was shown especially beneficial in types that were able to overtop possible competitors (Weinig, 2000b). This coincides with the observation in our model simulations. Plastic plants, which invested in height at a later stage of development, could attain a larger height than plants with large initial height growth investment.

In the simulations with varying density, it was found that the evolutionary stable height investment increased with density. This phenomenon is described extensively in the literature. It arises frequently as a phenomenon in empirical studies (Schwinning & Weiner, 1998) and also in other game-theoretical studies on the adaptive value of height, like Givnish (1982) and Iwasa et al. (1984). Nevertheless, the explanation of the exact

cause for this pattern is usually not clear. In our study we found two reasons for the better performance of plants with a large height investment at high densities. With an increase in density, the intercepted light per plant diminished. Because lower plants already receive relatively less light because of shading, these plants experience this more strongly than higher plants.

However, the fact that taller plants shade lower plants more severely at higher densities is not the only reason why the ESS was of greater height in denser stands. When competition for light is very strong, the possession of a large leaf area benefits plants less because a large part of this leaf area is shaded while at the same time it requires carbon for maintenance respiration. Leaf area thus becomes a respiratory burden at high density. Because carbon cannot be simultaneously invested in stems and leaves, taller plants will have relatively smaller leaf areas. With a lower leaf area, plants with higher height investment perform better at higher densities than plants with a lower height investment, even aside from the overshadowing of plants with lower height investment.

As already stated, we found that with increasing density, a type with higher height investment was an ESS. This meant that, at each different density, another height investment type was fittest. When we introduced an explicit space, it allowed for differences in local density. The fitness of types did no longer depend solely on the encounters with other types on basis of their frequency, but also on the specific density at which these encounters occurred. With a random distribution of individuals in the environment, there were stochastic differences in plant density per patch. This allowed different height investment strategies to find a 'window of opportunity'. This prevented the exclusion of these types from the area. Up to four types could stably coexist. It is interesting to consider that the prerequisite for the coexistence, namely the differences in density per patch, will occur in any population exhibiting (random) distribution of individuals. Different height investment types, if able to evolve, could establish and persevere under such simple conditions.

In a natural field, the canopy is usually divided in two or more distinct layers (Mitchley, 1988; Liira & Zobel, 2000). The height distribution that emerged in the simulation with explicit space resembled a height distribution as can be found in a natural field. On closer inspection however, the height distribution was brought about by a different mechanism. Whereas in a natural field each layer contains species of comparable growth shapes, in our model each layers consisted of a mixture of all height investment types. In our simulations, the layers developed because the each of the plant types were of low stature at some densities and tall at other densities. This shows that it is important to examine the mechanisms behind found patterns, before a statement is made on the realism of a model.

**SEED MASS INVESTMENT
AS A MECHANISM FOR COEXISTENCE**

Summary

Plants within natural communities are highly variable in their timing and extent of reproductive effort. In this study we analyse the adaptive value of different timing of seed investment. For this purpose, a mechanism-based game theoretic model is used. It was found that a switch to reproduction in the approximate middle of the growing season gave the highest fitness in single isolated plants. A later switch increased competitiveness but decreased seed output. Under the influence of two-sided competition, plants should postpone the switch to reproduction to slightly later than the switch of the competitor to attain maximum fitness. In an evolutionary context, this phenomenon caused plants to evolve from an early to a late switch to reproductive investment, even though an earlier switch in principle gave higher fitness to the population. The trade-off between vegetative growth and reproduction thus caused a ‘tragedy of the commons’. It was found however, that there were cyclic opportunities for extinct types to re-establish themselves in the community. We propose that a simple life-history trade-off as presumed here between growth and reproduction can generate dynamics within a community so that diversity of types is maintained, and this process is characterised by large fluctuations in abundance of different types over the course of years.

Keywords: timing, phenology, seed production, trade off, competition, population dynamics

Introduction

In life history theory, reproductive output is one of the main determinants of fitness. This is because reproductive output has a great impact on the rate of increase of a genome in a community. Since it is such an important component of fitness, the allocation scheme determining reproductive output should be subject to strong selection. One would expect all plants to evolve towards a single or at most a few optimal reproductive allocation schemes (Schmid & Weiner, 1993). Reproduction in higher plants however is extremely variable in terms of its timing and extent (Reekie et al., 2002) and this influences the reproductive success (Kawecki, 1993; Biere 1995). In literature on reproductive output, a lot of contrasting theories exist on the reasons for this variability (Willson, 1983). Most empirical and theoretical studies have focussed on the hypothesis that plants segregate their flowering temporally to minimise inter specific overlap in flowering times and thus ineffective pollination or competition for pollinators. This hypothesis is however rarely supported by experimental or field studies (Shmida, 1981; Sakai, 2001; Martinkova et al., 2002). Another hypothesis is that segregation of flowering time should be advantageous for an inferior competitor, as it may result in relaxed intra-specific competition during seed colonisation of empty sites. Also, the hybridisation of types may be prevented. Another explanation might be that internal constraints of plants have indirect effects on the success of reproductive phenology. Genetic correlation of different traits can slow down or prevent the evolution to the optimal value of a particular trait (Conner, 2002). Trait assemblages within a type can do the same. When types, for whatever reason, have developed a different resource allocation pattern, an additional investment might be beneficial for one type but unfavourable for the other. One type may adapt the additional strategy whereas the other type may not. Differences in allocation patterns of types can thus result in alternative combinations of life-history characters. This may also apply for reproductive allocation strategies and thus explain the multiplicity of different reproductive allocation strategies (Lovett Doust, 1989; Dorn & Mitchell Olds, 1991).

With all these available theories, it would be interesting to perform a study on the direct influence of reproductive allocation on plant fitness. This way it can be evaluated whether underlying allocation schemes without additional mechanisms have adaptive value and can contribute to the diversity in reproductive allocation schemes. These basics have been largely overlooked in the search for the adaptive value of different reproductive allocation schemes. In this chapter the focus will be on the adaptive values of the extent and timing of reproductive allocation.

Reproductive output of a plant could be seen as the product of plant size and its reproductive allocation (Sugiyama & Bazzaz, 1998). Biologists have often argued that fitness will be enhanced if an organism can develop more rapidly and grow to a larger size before making the transition to reproductive maturity (Ollerton & Lack, 1998; Callahan & Piglucci, 2002). Growth and size of the plant is, in this view, determined by environmental conditions, like for instance resource availability. This has to be seen as an effect separate from the reproductive allocation scheme of a plant (van Noordwijk & de Jong, 1986). Namely, with a fixed amount of resources, the allocation to reproduction is

subject to a trade-off with the allocation to vegetative growth, as in many plants both investments are drawn from a common carbon pool (see review of Obeso, 2002). A difference in allocation scheme will lead to a different reproductive output, irrespective of the environment.

As plants mostly grow in close proximity of each other, most often competition will play a role in affecting the fitness of plants with different growth strategies (Weiner, 1988). Especially in dense stands, competition will be a main determinant of the magnitude and direction of selection. Competition will first of all affect the nature of the trade-off between reproduction and growth. Plants under the influence of competition will generally have reduced rate of development and growth (Callahan & Pigliucci, 2002). An increase in resources allocated to reproduction carries with it a reduction in growth, increased risk of death and the accompanying risk of losing further opportunities to reproduce should this occur (Lovett Doust, 1989). Competitive vigour may determine the success of an individual. A bigger plant size would give a plant an advantage in resource acquisition over smaller plants, while at the same time denying these smaller plants the contested resource. Initial size differences will thus tend to increase in time. Considering this, plants may benefit from a large (initial) vegetative growth. On the other hand, plants may also benefit from early reproduction in a competitive setting. With an early reproduction, the period of reproductive investment is lengthened and the potential for high reproductive output is enhanced. Also it is a strategy to avoid having no reproductive output when a sudden or early death occurs. Plants in deciduous forests for example have evolved early reproduction, thus making use of the temporary beneficial light climate in early spring before the canopy closes (Werger & van Laar, 1985). Both timing and amount of reproductive allocation will have large effects on fitness of competing plants.

To get a better understanding on the growth / fitness relationship, the whole dynamic process of allocation to growth and reproduction should be taken into account. Also, the effect of competition will shed light on evolutionary pressures and the (un-)possibilities of a large diversity of plant allocation schemes. In this chapter we will try to elucidate the adaptive value for plants with different reproductive allocation patterns in a game theoretical framework. This method has proven to be fruitful in the research of timing issues (Iwasa & Levin, 1995; Morbey & Ydenberg, 2003). We will see whether, with the mechanistic approach taken, we can gain some understanding on the optimality of strategies and the performance of strategies in a competitive setting. In this chapter, we will first investigate the optimal timing of a switch to seed mass production in single isolated plants. Next, the influence of competition with other types is studied, when types compete in a pair-wise setting. Finally, we extend this simulation to multiple competing plants.

Methods

To simulate the fitness and growth of competing plants of different types we use a mechanistic plant growth model. The model is described in detail in Chapter 2. Only a

brief description of the most important features, and the extensions of the model are given here.

The light climate

In this chapter, a seasonal fluctuation in the yearly light climate is introduced, as we would expect it to occur in a temporal region (Kirschbaum, 1999):

$$\text{Daily Incidence } I_{veg} = I_{mean} + I_{amp} \cdot \sin \left[\Pi \cdot \left(\frac{t - 0.5 \cdot year + 0.25 \cdot year}{0.5 \cdot year} \right) \right] \quad (5.1)$$

Here I_{veg} is the daily incident light above the canopy at day t in the simulation year, I_{mean} is the mean incident light above the canopy during a year and I_{amp} is the amplitude of the fluctuation in incident light.

Table 1. Values of yearly fluctuation of incident light, used as parameters for formula 5.1.

Length of year (days)	Amplitude irradiance	Mean irradiance (ppfd/m ² /s)	Period of irradiance (sec/day)	Resulting mean day-sum (ppfd/m ² /day)
365	1360	1700	25200	42.84 * 10 ⁶

The growth of plants

All plant types consist of three basic structures: leaves, roots and a stem. Aside from these structures the plant produces seed, which is used as a measure for plant fitness. At some point in its lifetime, the plant switches from purely vegetative growth to purely seed production. Each plant type starts with an initial leaf area, root mass and height. From the start of the simulation, the plant intercepts light, photosynthesises and grows. There is a particular order in which the carbon attained from photosynthesis is partitioned. First, carbon is used for maintenance respiration, expressed in gram carbon per unit structural mass. Then, if any carbon is left, and the plant is not in the reproductive phase, the requirements for growth are met. With the construction of structural mass a constant amount of carbon per unit mass is respired (i.e. construction costs). We assume the plants allocate a fixed fraction of their carbon to height growth. All plants in the simulations in this chapter have a constant height investment of 0.175 (gram carbon per gram carbon of net photosynthetic production) when growing vegetative. This was the optimal height

allocation as found in Chapter 4. As the plant grows in height, the leaves at the base of the plant are discarded while leaves at the top are newly produced to maintain the shape of the plant's canopy. All plants have a symmetric leaf area distribution over height. It is assumed that the carbon, imbedded in the leaves and roots, is only partly retractable. The reallocation of leaves with height growth thus implies an extra cost. Whatever carbon is left after height growth is invested in leaf area and root mass in some constant proportion. If the carbon balance after maintenance or height growth is negative, leaf area and root mass are shed and the retracted carbon from this leaf area and roots is used to make the carbon balance equal to zero. If either leaf area or root mass is zero grams or less, the plant is considered dead.

The switch to seed production

Cohen (1971) and Iwasa (2000) made mathematical models on seed mass production with a fixed season length. They showed that, to achieve an optimal allocation scheme that maximises seed mass yield, plants should show a sharp transition between vegetative and reproductive phases of growth. Iwasa (2000) showed that in terms of seed mass, a less sharp transition would always be sub-optimal. The seed production strategy that we explore is a strategy in which there is a clear switch from vegetative growth to seed mass production. It is assumed that within this strategy, maintenance of current biomass is a priority. This is paid from net photosynthetic production. In the simulation on single isolated plants, this means the plant is able to maintain its shape when it has switched to seed mass production. Leaf area and consequent light interception changes only if the plant is forced to shed leaf area as a result of a diminishing light climate.

We refer to this strategy as the Time Based Switch (TBS) strategy. Plants can either switch to seed production at an early stage or switch at a later stage during the growing season. To evaluate the importance of the timing of a switch to seed production, different types are distinguished within TBS strategies. The types differ in their timing of a switch to seed mass production, based on time passed since germination (Table 2).

Table 2. Different types within Time Based Switch (TBS) strategies to seed mass production.

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7	Type 8	Type 9	Type 10
Timing (day)	5	25	45	65	85	105	125	145	165	185

Both early and late investments in reproduction have benefits and drawbacks. Plants that switch to seed mass production at an early stage have a long period for seed mass

production. However, these plants have not yet produced much leaf area. They cannot intercept much light and gross photosynthetic production will be small. It is better to delay seed production until a larger leaf area has been produced. Plants that switch to seed mass production at a very late stage have produced much leaf area and will have a large gross photosynthetic production. These plants nevertheless may produce a low amount of seed mass for a number of reasons. Firstly, the time until the end of the simulation period is near and seed mass production period is short. Secondly, plants have more leaf area and have a higher degree of self-shading. Thirdly, being larger, the plant will have high costs of maintenance and not much carbon will be left to invest in seed mass. As a result, the optimal switch timing for single isolated plants should be expected somewhere in the middle of the season. Many authors found that there is a single optimum for a switch to seed mass production for plants in a finite growing season (Widen, 1991; Iwasa, 2000).

Table 3. Advantages of timing of a switch to reproduction. Pluses depict the degree of advantage of a particular switch time (early, middle, late) to the listed processes.

	Early	Middle	Late
Period of reproductive investment	+ + +	+ +	+
Gross photosynthetic production	+	+ +	+ + +
Net photosynthetic production	+ +	+ + +	+
Competitive vigour	+	+ +	+ + +
Reproductive success in case of sudden death	+ + +	+ +	+

Results

Single plants that switch to seed mass production

The performance of TBS strategy types is evaluated on the basis of their produced seed mass. In Figure 1 are the leaf area production and the produced seed masses per plant type per strategy for single isolated plants. As predicted, there is an optimum in produced seed mass for a medium type. In TBS types the optimum seed mass yield is achieved when switching to seed mass production at 105 days after the onset of growth (this is TBS type 6 in Figure 1).

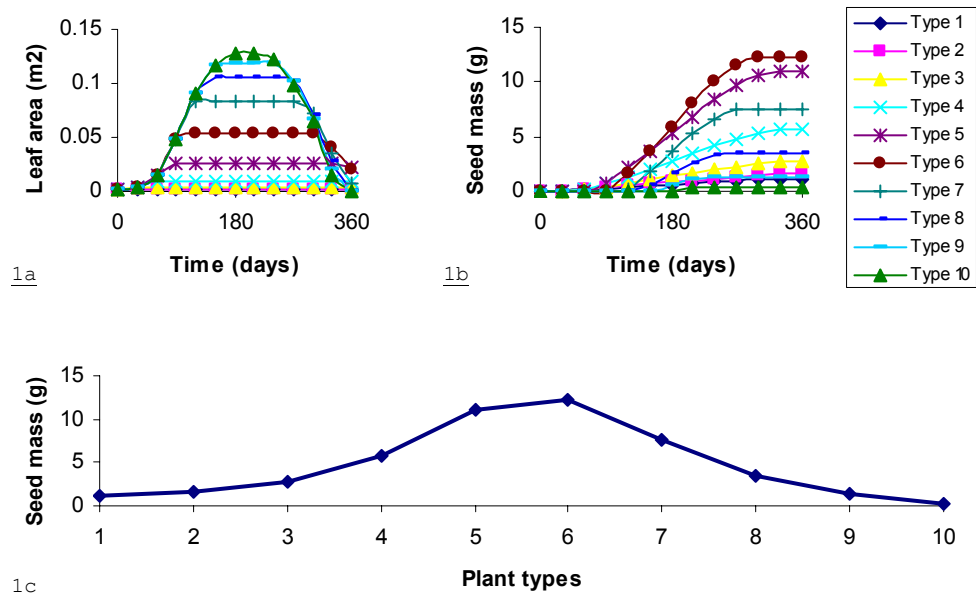


Figure 1. Leaf area development of different TBS types (a), seed production during one simulation period (b), and seed mass production of different TBS types at the end of the 365-day simulation period (c). See Table 2 for a description of types.

The differences in produced seed mass at the end of the simulation period are quite distinct. Type 6 has the largest seed mass. In population development, the type with the highest seed production will increase at the disadvantage of types with a lower seed mass. Types 1 to 5 and 7 to 10 would thus be excluded fast in population development for these single isolated plants. In pair-wise competition however, different qualities are important. A plant has to cope with its neighbour besides optimising its own fitness and a different type might achieve the highest seed mass.

Competition and the switch to seed mass production

Because plants usually are in close proximity, competition is likely to play a role in the fitness of seed investment strategies. Plants that switch to seed mass production early will have low investment in vegetative structures. This may diminish the competitive vigour of the type. On the other hand, types with a late switch might produce little seed and lag behind in fitness. Will TBS type 6 continue to perform well in a competitive setting? Will one type perform best against all competitors, or will the success of a type depend on the type of competitor it encounters?

There have been many studies on the effect of competition on the timing of a switch to reproduction. Results however have been rather contradictory. Many studies report a delay in reproductive investment under the influence of competition. Plants might be selected for delaying reproductive investment in favour of vegetative growth and increased competitive vigour. For instance, annual plants were found to have a delayed reproduction if grown at high density (Waller, 1988). However, whether such a reaction is adaptive is not certain. It may well be a non-adaptive trait, because light interception and consequently development may be slow in competing plants, causing plants to have delayed reproduction (Weiner, 1988; Pino et al., 2002). For instance, Stanton et al. (2000) and Dorn et al. (2000) found that although plants flowered later in time with light limitation, the phenotypic response was to actually flower earlier in development. Several studies have found plants to start reproduction earlier as a result of shading. Mirmirani & Oster (1978) found in their simulation study that competition enforced earlier switching times. Botto & Smith (2002) and Callahan & Pigliucci (2002) found an acceleration of flowering as a response to shade in *Arabidopsis*. Biere (1995) observed precocious flowering under low resource availability in a perennial meadow species. In forest under story plants it is well known that plants develop early in the season in order to avoid shade cast by trees. The proposed mechanism is that the potential for growth declines and plants can even decrease in leaf area or die when a competitor casts shade on a plant. This would be detrimental for a successful reproduction. For plants it is beneficial to switch to seed mass production before shade becomes more severe and possibilities for reproduction decline. As plants are more fecund at larger size, they will delay reproduction in favourable environments. In unfavourable environments plants will have early reproduction (Galloway, 1995) as a stress avoidance strategy. It is much more likely that this is an adaptive trait.

If we want to explain the diversity in plants from adaptive value, a condition is that the different switch types have an advantage at some point in community development or at steady state over (some of) the other types. We will investigate the timing of different types under conditions of competition, and check whether these are advantageous and have adaptive value.

To answer these questions, we let the different TBS strategy types (described in Table 2) compete in every possible combination. Every realised seed mass at the end of simulation of a type in combination with another type is put into a ‘pay-off matrix’ (Riechert & Hammerstein, 1983). The matrix is constructed as follows:

$$\text{Pay-off Matrix} = \begin{bmatrix} p_{ij} & \cdot & \cdot & \cdot & p_{in} \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ p_{nj} & \cdot & \cdot & \cdot & p_{nm} \end{bmatrix} \quad (5.2)$$

Here p_{ij} is the pay-off of plant type i competing against plant type j . In total there are n plant types.

Depicted in Table 4 and Figure 2 are the seed productions of competing types in different combinations. In the rows of Table 4 are the pay-offs of different target types against a particular opponent type. Within a row, the target type that has the highest seed production against a particular opponent is written in bold. In the columns are the pay-offs of a target type against different types of opponents.

Table 4. Seed output (gram per plant) of TBS target plant types in pairwise competition with TBS opponent plant types. The highest seed output, within a row, of a target type against a particular opponent type is written bold. For a description of types, see Table 2.

Opponent	Target Plant types									
	1	2	3	4	5	6	7	8	9	10
Type 1	1.15	1.53	2.62	5.47	10.78	12.37	7.61	3.53	1.30	0.33
Type 2	1.13	1.50	2.54	5.32	10.61	12.41	7.69	3.56	1.32	0.33
Type 3	1.09	1.45	2.42	5.01	10.23	12.49	7.85	3.64	1.34	0.34
Type 4	0.97	1.29	2.15	4.42	9.15	12.52	8.27	3.85	1.42	0.36
Type 5	0.64	0.84	1.41	3.03	6.58	10.66	9.56	4.58	1.69	0.44
Type 6	0.15	0.18	0.23	0.32	2.05	5.60	7.96	6.86	2.66	0.73
Type 7	0.15	0.18	0.23	0.31	0.33	0.66	3.22	5.06	5.33	1.78
Type 8	0.15	0.18	0.23	0.31	0.33	0.27	0.23	1.50	2.98	4.16
Type 9	0.15	0.18	0.23	0.31	0.33	0.27	0.20	0.14	0.56	1.50
Type 10	0.15	0.18	0.23	0.31	0.33	0.27	0.20	0.14	0.09	0.14

Table 4 shows that the optimal type in terms of seed mass production differs with the type of opponent. The types with the earliest switch to seed mass always perform badly; there is no opponent type against which they are the optimal type.

Figure 2 gives the visualisation of Table 4. On the front axis are the plant types for which the seed mass is depicted. On the right axis from back to front are the types they competed against. The lines from left to right thus depict the seed mass of different TBS types (on the front axis) when competing with a particular TBS type (on the right axis).

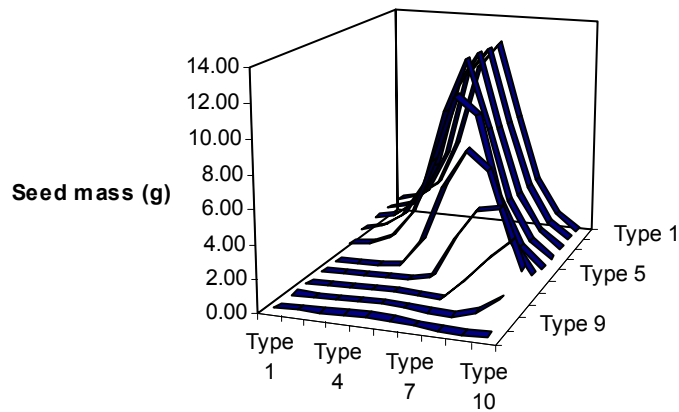


Figure 2. Visualisation of the seed output Table 4. Seed mass of time-based seed timing types. On the x-axis (front axis) are the types for which the seed mass is depicted. On the y-axis (right-hand axis) are the opponent plants. See Table 2 for a description of plant types.

The performances of types competing with a plant type that switches very early, such as type 1 (rear end line in Figure 2), show that type 6 type achieves the most seed mass. In competition with later-switch types (lines more to the front in Figure 2) we see that the optimum shifts towards the right. This implies that types should delay their investment in seed mass when competing with types that are also late in seed mass production. This however gives a lower seed output for both plants.

The cause for this shift towards later seed mass investment lies in the highly asymmetric competition between the plants. As long as a plant can interfere with its competitor, the competitor cannot grow fast. When plants delay their seed mass production, they can develop a big vegetative mass and this means also a large leaf area. If a plant starts earlier with the production of seed mass than its competitor, it becomes overshadowed. The amount of intercepted light is reduced and seed mass production rate decreases for this earlier switcher. During the time that the late switcher still increases in vegetative mass, the early switcher has less and less to invest in seed mass production. It can even become so severely overshadowed that it cannot intercept enough light to pay for maintenance. This forces it to shed leaves and roots, leading to an even quicker pace of deterioration. When a plant has to compete with an early switcher, the best strategy is to switch early also. Nevertheless, the plant should switch to seed mass production at a slightly later stage than its competitor. In short, a switch to seed production should be shortly after the switch of the neighbouring plant.

The most important conclusions that can be derived from Table 4 and Figure 2 are that the optimal timing of investment in seed depends on the type of competitor. Generally it is best for plants to switch relatively early to seed mass production, but

always slightly later than the competitor to avoid competitive suppression. A later switch, however, will go at the cost of seed mass production.

An interesting question now is how these types will fare if we assume a community in which all types are present. In this community, all types can be encountered. The performance of a type now does not only depend on the kind of neighbours it encounters, but also the frequency at which these different encounters take place. In Table 5 are the summed seed productions per type when competing with all possible opponent types, assuming all types are present at equal abundance.

Table 5. Total seed output per TBS type, summed over all combinations with opponent types (columns in Table 4). All types are assumed equally abundant. For seed output per combination, see Table 4. For a description of types, see Table 2.

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7	Type 8	Type 9	Type 10
Seed mass	5.73	7.50	12.30	24.79	50.70	67.52	52.78	32.85	18.68	10.10

From Table 5 can be derived that, totalled over all competitors, type 6 has the highest pay-off. But will type 6 still be superior if the frequencies of types change?

Multiple competing types

The average total pay-off ‘*P*’ for a target plant type *i* that is present at a certain frequency *f* can be calculated as the summed total of the plant type’s seed output while competing with different opponents *j* which are present each at their own frequency:

$$Pay\text{-off of target plant type } i \qquad P_i = f_i \cdot \sum p_{ij} \cdot f_j \qquad (5.3)$$

The pay-off against an opponent plant type is *p_{ij}*. We assume an infinitely large plant stand with a certain composition of types. *P_i* is then the average pay-off of the target plant type *i* competing with the types present in the stand, during one single simulation year.

In addition, we can calculate whether the type will increase or decrease in frequency in the course of years, compared to other types. For this we scale the total amount of attained seed mass for each single type to the total amount of seed mass produced by all types present. Now the frequency in the next generation of target plant types can be calculated. The new frequency is the relative contribution of the target plant’s current pay-off to the current total pay-off of all competing plants:

$$\text{New Frequency of target plant type} \quad f_{it+1} = \frac{P_{it}}{\sum P_{jt}} \quad (5.4)$$

With each repeated calculation, the relative frequencies of plant types in the community will change in the way described above. The frequency development for all types can now be followed during simulation years. The pay-off per type will differ with each change in the composition of the community.

According to Formula 5.3, the seed mass production of a type depends on the types that are encountered as well as the frequency of these encounters. If all types would be equally abundant, type 6 would have the highest overall seed production (see Table 5). As a consequence, this type will initially increase most in relative frequency. Depicted in Figure 3 is the frequency development over several years of competing TBS types 1 to 10. If the frequency of a plant type drops below a certain threshold frequency (10^{-5}), the type is supposed to be extinct and its frequency is set to zero.

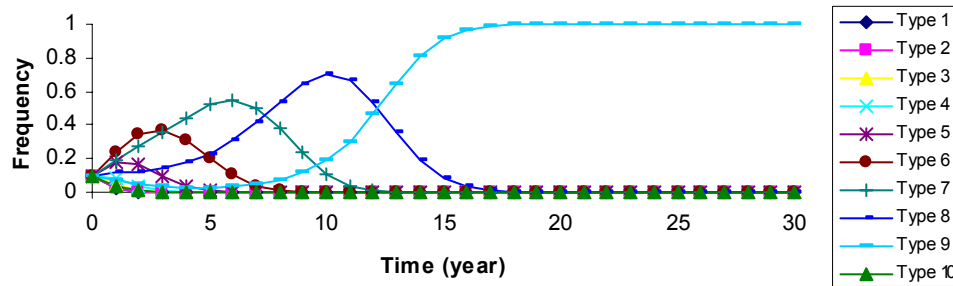


Figure 3. Frequency development of competing TBS plant types. For a description of types, see Table 2.

The frequency graph (Figure 3) shows that there is an initial shift in dominance during the simulation. Initially, when all plants start with equal frequency, type 6 that invests relatively a lot in seed mass is the most dominant. During the next calculations, types 1 to 5 that invest earlier (and thus loose of this type in competition) go extinct. Type 6 now encounters relatively more late switching plants, which have a larger competitive vigour. These more competitive types increasingly suppress type 6 and its seed production declines. The next type, which is type 7, invests a lot in seed mass but has a slightly better competitive vigour than type 6 and thus replaces type 6. As can be seen in Figure 3, alternately SPI type 6,7,8 and 9 are the dominant type. There is thus a succession of types. The type that eventually becomes all dominant is TBS type 9. This type 9 switches to seed mass production at day 165.

Figure 4 shows the average seed mass per plant during the frequency development.

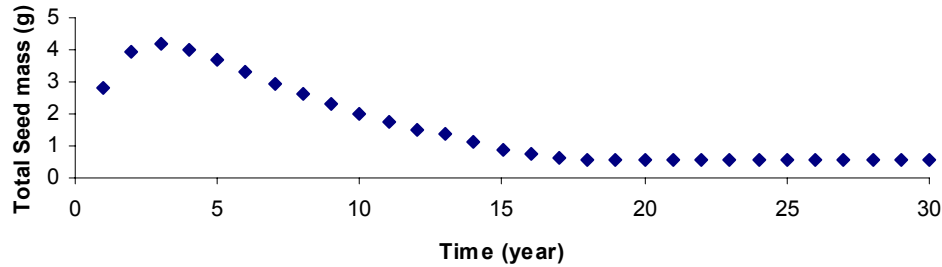


Figure 4. Seed mass production per plant during development of the community, averaged over all individuals of all types. For frequency developments per type, see Figure 3.

Initially, the average seed production increases slightly. This is because the very early switch types go extinct. These types produce a low amount of seed because they start allocation to reproduction before the optimal switch timing, and additionally all other types suppress them. After the initial increase, the average seed production gradually decreases to a low level. This is because later switch types increase in frequency. These types produce a low amount of seed because of their late switching time.

It is logical to assume that if a plant produces more seed mass than other plants in a vegetation stand, its frequency will increase in the next generation. It does not follow, however, that the total seed production of the vegetation would necessarily become even higher as the whole community is progressively made up of more productive plants in terms of vegetative biomass (Zhang et al., 1999). In Figure 4 the total seed mass production of all types is combined, in gram seed per year. In this figure it can be seen that the population of TBS types that is dominant at the beginning of the simulations produces far more seed mass than the TBS types that is selected for eventually. This is a classic example of a ‘tragedy of the commons’ as introduced by Hardin (1968). In the case of dealing with plants, it can also be called ‘growth redundancy’ (Donald, 1968). Donald (1968) argued that in crops the most competitive individuals would gain a disproportionate share of a limiting resource in the environment, and would thus be favoured by natural selection. He proposed that natural selection through competition would generally result in ‘over-growth’ of some resource-foraging organs. Because investments are drawn from a common carbon pool, carbon invested in resource harvesting organs cannot be invested in seed production. Types with such large sized organs may thus not have an optimal seed mass production, but rather suppress neighbouring plants so that these have an even lower seed mass production than the plant with over-growth. Gersani et al. (2001) showed this to be true for plants competing for limited root-space (and thus nutrients and water). Schieving & Poorter (1999) showed that

species would increase specific leaf area in a competitive game, at the expense of carbon gain. Kawecki (1993) found in his model study that in a competitive situation, plants should mature later and at larger size than what maximises the fitness measure. In our model plants, we see the same phenomenon occurring. If all plants would be of TBS type 6, which is optimal in terms of seed mass yield in single isolated plant growth, yield of the community as a whole, would be maximal. However when a ‘cheater’ is introduced in the vegetation that invests less in seed mass and more in overall growth, seed mass output of this ‘cheater’ relative to the other plant types is higher because it suppresses the other types in competition. As a consequence the seed mass output of the community as a whole diminishes as the ‘cheater’ increases in frequency. We see a clear succession from the optimal type towards types with higher vegetative mass.

Dorn & Mitchell Olds (1991) found, in *Brassica campestris*, that populations may evolve to become early flowering and small or late flowering and tall. We don’t know the reason why, in their study, plants in the different populations remain small or became tall. It correlates however with our results. In our model the best strategy for a population of small plants is to have an early switch to seed mass production (optimal strategy) and for a population of large plants the best strategy is to have a late switch to seed mass production (tragedy of the commons). Possibly, in low competitive environments, plants will develop towards an early switching strategy.

On the controversy in literature

In literature on the timing of a switch to seed mass production, both acceleration and delay of flowering is recorded when plants compete for light. How is it possible that such contrasting effects are recorded as a result of competition? The answer may be in the type of competition: one-sided or two-sided. In the case of two-sided competition (both plants shade each other), it is best to interfere with your neighbour as much as possible, to reduce the asymmetry of competition. For that purpose, seed mass investments should be delayed. This is a mechanism that will invariably lead to a tragedy of the commons. This mechanism is what we observe in simulations done in this chapter. One-sided competition is the case when a taller plant shades a focal plant, but the focal plant does not shade the taller plant. When the tall plant grows, the light climate for the focal plant is diminished and the total amount of light harvested over the growing season is less. The optimal timing of seed mass production will consequently be at an earlier stage (Cohen, 1976). In Figure 5 we show that for a plant that is subject to one-sided shading, the time to start seed mass production becomes earlier when the severity of shading is increased. For the simulations of Figure 5 we introduce a plant with a high initial height and leaf area and a high leaf area position on the stem, instead of the equal starting characteristics we used in previous simulations. Between this large plant and the TBS type plants there is very little overlap in leaf area at any height. Competition in this way is almost completely one-sided.

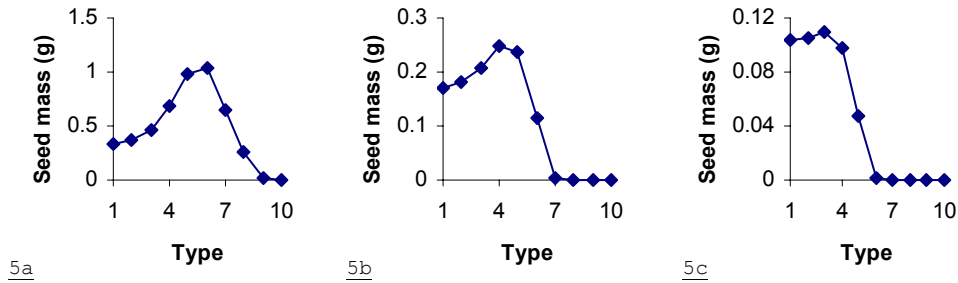


Figure 5. Seed production for TBS types subject to different levels of shading. For a description of types see Table 2. Shading levels were achieved by varying the seed investment of the overshadowing plant, causing it to invest less in leaf area.

a: low shading (0.7 seed investment of the overshadowing plant), b: medium shading (0.5 seed investment of the overshadowing plant) c: high shading (0.0 seed investment of the overshadowing plant)

For the different simulations we varied the seed mass investment ratio of the large plant. With a large seed mass-investment, a plant was created that had little carbon for overall growth. Consequently, growth was slow and this resulted in a small leaf area during the simulation. This resulted in low shading for the TBS strategy plants. The optimal timing of reproduction was late (Figure 5a). With a small seed mass-investment, we created a large plant that could invest a lot of carbon in overall growth, which resulted in a fast growth and a large leaf area during simulation. This resulted in a heavy shading of the TBS strategy plants. The optimal timing of reproduction was earlier (Figure 5b). With no seed investment, the overshadowing plant had yet faster growth and leaf area. Optimal timing of reproduction shifted to a still earlier timing (Figure 5c).

Reintroduction of plant types

Until now, types that went below a certain frequency were supposed to go extinct. It is very interesting to see whether the remaining seed investment types are evolutionary stable strategies. What happens when extinct types are enabled to make a re-entry? We can think of several mechanisms in nature that could cause this the re-entry of locally extinct types. A seed bank enables types to remain dormant until environmental conditions are favourable (Pons, 1991; Willems, 1995; Kalamees & Zobel, 2002). Recruitment of types from nearby source populations could occur on a regular basis. Also we could assume regular mutations, so that types could return from extinction by means of mutations. In all cases, reintroduced types can persevere only if there is a positive growth rate for these types arriving at low frequency. To simulate this, the frequency of types is not set to zero at extinction, but is maintained at a very low frequency (one

millionth part of the total community size). It can be assumed that the types at this low frequency have no important influence on the calculation of dynamic pay-off for types at higher frequencies. Figure 6 shows the frequency development of the different types.

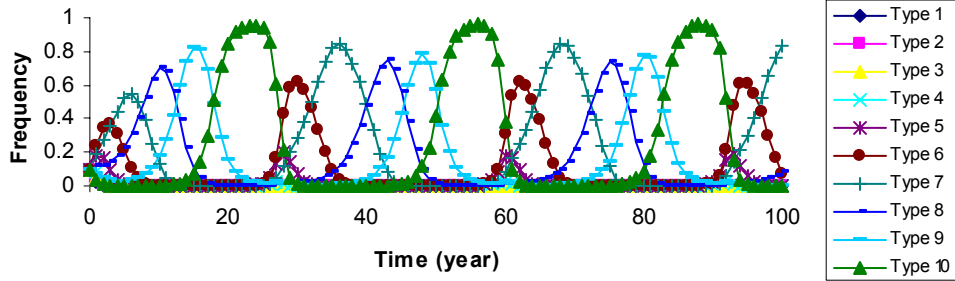


Figure 6. Frequency calculations on TBS type plants, including reintroduction of types. See Table 2 for a description of the distinguished types.

Results show that the introduction of formerly extinct species is successful. The frequency development of TBS types with reintroduction shows a regular pattern of decreasing and increasing species in the course of years (Figure 6). Apparently, there are cyclic opportunities for species for reintroduction. This might be a mechanism for maintenance of species diversity.

The cause for this continual succession lays in the fact that the evolutionary ‘stable’ TBS type 9 produces little seed mass and even less when competing against another TBS type 9 (see Table 4). At some point in frequency calculations, the frequency of plants of type 9 is very high and it encounters con-specifics at a high frequency. The performance of TBS type 10 plants against a TBS type 9 is relatively good (see Table 4). In the previous simulation these type 10 plants were already extinct, but with reintroduction they can make a re-entry. As type 9 and 10 increase in frequency total seed production is decreasing and opportunities arise for type 6 to perform well. This type has a large seed production compared to type 10 and 9. When type 6 increases in frequency, it encounters more con-specifics and this confers an even higher seed production (see Table 4). Because type 6 is present, type 7 can perform well. It can outcompete type 6 and increase in frequency. This is followed by type 8 and the cycle, as explained in the case without reintroduction, repeats itself.

So far, we have taken only 10 types that differed 20 days in their switch to seed production from each other. If the types are taken closer together, even more types can coexist in a cyclic manner. We distinguish 27 types that differ 10 days in their switch to seed production. The total range of seed switches is from 5 to 275 days after the onset of

growth. In Figure 7 the frequency developments of the 27 types are shown. Only the first 250 years of simulation are depicted, after this the pattern repeats itself again.

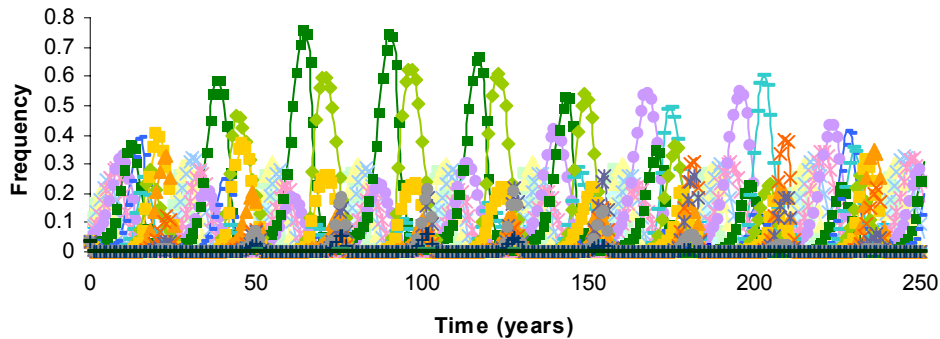


Figure 7. Frequency developments of 27 TBS types, differing 10 days in the switch to seed production. The timing of the switch to seed production varies from 5 to 275 days after the start of the growing season.

It is interesting to note that this rather spectacular result is obtained from a simple trade-off between vegetative growth and seed production. What is also important to realise is that these intricate patterns are generated from the vegetation development itself, and not by any external process such as disturbance. Besides the intuitive explanation given for the ability of species to reinvade a community, we can analyse the invasive ability of types in a more formal way. This method is described in the appendix.

On the basis of our simulations we conclude that a possible source of diversity in annual plants is the timing of seed mass production on a basis of time since emergence.

Discussion

In this chapter the aim was to investigate the advantages and possible adaptive values for different seed investment strategies, thus explaining the diversity of these strategies in herbaceous annual plant communities.

In our simulations, plants invest carbon from net photosynthetic production in seed mass (Fernandez & Warembourg, 1987; Bouwmeester et al., 1995). Iwasa (2000) and Cohen (1971) assumed this strategy for simulations on optimisation of growth. Because it is a likely strategy for annual plants we have chosen this strategy as our model strategy. Reekie & Bazzaz (1987b) showed that the type of currency is not so important. In their study, carbon reflected the investment of other nutrients as the carbon costs increased with limitation of other nutrients. However, it should be noted that this is not

always the case and sometimes seed production is limited by nitrogen (e.g. Witkowski & Lamont, 1996). The most limiting resource will dictate possible trade-offs in allocation. Because, in our model, we assume nutrients like phosphorus and nitrogen to be in ample supply to the plant, carbon will be a good currency.

With interference competition, plants adapted to a later timing of reproduction. Various other authors showed this phenomenon as well (Donald, 1968, Kawecki, 1993; Zhang et al., 1999). Strong selection for growth is among the key processes for an adaptation for delayed reproduction (Rees & Rose, 2002). Because the competition for light is asymmetric, it is important for plants to gain a larger stature than their competitor. The plant can cast more shade on its competitor will produce more seed relative to the competitor. Nevertheless, other studies reported an earlier timing of reproduction under the influence of competition. This could be a result of one-sided competition. Crowns of competing plants are separated in this case. A tall plant shades a lower plant but not the other way around. Because light becomes scarcer during the growing period when the tall plant increases its leaf area, subordinate plants will adapt to an earlier timing of reproduction under the influence of this kind of competition.

Second it was found that when there is asymmetric competition in plants, and plants are subject to a trade-off between the production of vegetative mass and reproductive mass, population development of types will invariably lead to a 'tragedy of the commons' (Hardin, 1968; Kawecki, 1993). Plants that invest in growth for an extended period of time have less carbon to invest in seed. The community will go towards a population consisting of types that produce an excessive vegetative mass and only a little amount of seed mass. This can have large consequences for agricultural systems where often plants are bred for a large competitive vigour (Donald, 1968).

Recently, more and more evidence is found that plant populations can be cyclic or chaotic rather than converging to a stable equilibrium (Bauer et al., 2002). Several mechanisms have been shown to be capable of generating such a pattern. Non-linearity in responses seem to play a crucial role. In their modelling study, Silander & Pacala (1990) determined that low seed dormancy; high germination success, a minimum plant size threshold for reproduction or high soil fertility all increased the probability of oscillatory and chaotic behaviour. Bauer et al. (2002) found cyclic behaviour in the age-structure of simulated populations because of a monopolization of space by the larger age groups. Crone & Taylor (1996) found cyclical dynamics in a real plant population that could not be accounted for by changing environmental conditions. Their pattern is a result of populations cycling from high to low density, possibly is a result of overcompensation in seed set (our note). We simulated large initial oscillations for species composition for plants differing in seed mass investment. We even found stable cyclic species replacement patterns when we allowed species to be reintroduced. Oscillations were caused by succession from highly fecund to highly competitive species. These patterns were generated not by external factors, but by the process of competition itself.

Empirical evidence for the occurrence of such large-scale fluctuations in species composition as we found in our model study, will not be easy to trace in real plant communities. One would need very long-term studies. Because long-term records are not

available for most experimental sites, this phenomenon would go undiscovered. The 'Park Grass experiment', however, is a long-term experimental set of equilibrium plant communities. Although monitoring showed the gross composition of the vegetation was at equilibrium over a 60-year period, annual records showed that individual species exhibited a range of dynamics (Tilman, 1996). Silvertown et al. (2002) argues that these cyclic fluctuations might be common phenomena in herbaceous plant communities, even those otherwise thought to be stable. They speculate that the cause of the sudden outbreaks of several species is momentary drought. Nevertheless they wondered how increases in the abundance of species were maintained for so long (for up to the complete period of 60 years) because the plants were short-lived. We propose that the simple life-history trade-off between growth and reproduction, mediated by competition, can generate such dynamics within a community, even without an environmental trigger.

Huisman & Weissing (1999) achieved oscillating patterns for plankton on the basis of competition for resources. The source of their patterns is based on Tilman's resource competition theory in which species are jointly limited by a single resource (Tilman, 1982). The minimum requirement of the contested resource is R^* . The species with the lowest R^* value will be the winner in competition. In their model, plants differed in their minimal requirement of a total of three different resources. If one type gets dominant, the resource it is most in need of will get scarce. Another species, with different requirements in resource ratio, would replace this competitor. A third will come in if the resource that the second species needs becomes scarce. Species thus displace each other in a cyclic fashion. They could even introduce a fourth species that could make use of the temporal variability in resource availability generated by the three original species. In this chapter, a similar cyclic pattern occurs for plant species that differ in the life-history trade-off between seed mass investment and growth. Just as Huisman & Weissing (1999) we show that an externally undisturbed community can produce its own disturbances to promote diversity. This might be one of the mechanisms that could explain maintenance of species diversity. We show that this is not restricted to a three-resource system but it occurs in a community that is limited just by light as a single resource.

In conclusion, it is interesting to note that with a simple allocation trade-off between vegetative growth and reproduction, such intricate patterns can be generated. It is also important to realise that these patterns emerge without external influences and are a consequence of the processes within the community. Thirdly, it should be noted that these patterns arise on the basis of competition for light as a single limiting resource. Lastly, it should be realised that the observed patterns are not caused by any mathematical property, but that they have a mechanistic basis.

Besides a switch to seed production based on time, we have also investigated a switch based on leaf area size. Types of the latter strategy showed a succession of types from high to low seed investment as well. One type became superior over all other types in the course of frequency development. However, for an annual plant that bases seed mass production on the size of its leaf area there is of course the danger that the plant does not attain the threshold leaf area and thus never starts seed mass production. This is exactly what we observed in late switching plants. When two late switching types

competed, they interfered to such an extent that both did not reach threshold leaf area before the end of the growing season. For annual plants this of course would be disastrous. If these types would compete with an earlier switcher, they would overgrow the early switcher by asymmetric competition and keep it at a low size. In this way late switching plants can reach threshold leaf area size needed for a start in seed mass investment. However, with an increase in frequency, the population of late switch plants would develop toward an evolutionary suicide. Probably there are not many annuals that solely base flowering on some threshold size of the leaf area. Plants that base flowering on size and lag behind in development will benefit from an additional environmental cue (Sachs, 1999).

Appendix

Aside from the intuitive explanation given for the ability of species to invade a community, we can analyse the invasive ability of types in a more formal way. We have the seed mass output ‘*A*’ per type for each pair of competing early and late seed investment plants. Suppose a matrix of two species, *S*₁ and *S*₂ (see Figure 8). We scale the pay-off of the types to *A*₂₂ (see Figure 9).

	<i>S</i> ₁	<i>S</i> ₂
<i>S</i> ₁	<i>A</i> ₁₁	<i>A</i> ₁₂
<i>S</i> ₂	<i>A</i> ₂₁	<i>A</i> ₂₂

Figure 8. Pay-off matrix of competing pairs of species.

	<i>S</i> ₁	<i>S</i> ₂
<i>S</i> ₁	α	γ
<i>S</i> ₂	β	1

Figure 9. Pay-off matrix of competing pairs of species, scaled to the pay-off of the competing pair *S*₂-*S*₂.

So that
$$\alpha = A_{11} / A_{22} \tag{5.5}$$

$$\beta = A_{12} / A_{22} \tag{5.6}$$

$$\gamma = A_{21} / A_{22} \tag{5.7}$$

The strategies are present each at their own frequency ‘*x*’. The frequencies of *S*₁ and *S*₂ add up to 1, which means that both frequencies can be expressed in terms of the other:

*Frequency of S*₁
$$x_1 = 1 - x_2 \tag{5.8}$$

*Frequency of S*₂
$$x_2 = 1 - x_1 \tag{5.9}$$

Produced seed mass per strategy is dependent on the frequency of the opponents and the frequency of the strategy itself:

*Seed mass S*₁
$$S_1 = x_1 (A_{11} \cdot x_1 + A_{12} \cdot x_2) = x(A_{11}x + A_{12}(1 - x)) \tag{5.10}$$

*Seed mass S*₂
$$S_2 = x_2 (A_{22} \cdot x_2 + A_{21} \cdot x_1) = (1 - x)(A_{22}(1 - x) + A_{21}x) \tag{5.11}$$

The frequency at the next time step for S_1 can be written down as the produced seed mass for S_1 divided by the total produced seed mass for both species:

$$x^+ = \frac{x(A_{11} \cdot x + A_{12} \cdot (1-x))}{x(A_{11} \cdot x + A_{12}(1-x)) + (1-x) \cdot (A_{22} \cdot (1-x) + A_{21} \cdot x)} \quad (5.12)$$

The difference between the current frequency x and the frequency at the next time step x^+ says something about the change in frequency of a species. If $x - x^+$ is positive the species has an increase in frequency. If it is negative, the species has a decrease in frequency. We take S_1 as an example.

$$x^+ - x = \frac{x(A_{11}x + A_{12}(1-x)) - (x(A_{11}x + A_{12}(1-x)) + (1-x)(A_{22}(1-x) + A_{21}x))}{x(A_{11}x + A_{12}(1-x)) + (1-x) \cdot (A_{22}(1-x) + A_{21}x)}$$

The divisor of the formula, which depicts the combined produced seed mass, has always to be positive by definition. So the numerator of the formula will determine what the sign of the change in frequency is. We try to clean up this formula. We multiply all terms by A_{22} / A_{22} and by doing so scale the pay-off to A_{22} as in formula 5.5-5.8.

$$x^+ - x = \frac{x A_{22} (\alpha x + \beta(1-x) - \alpha x^2 - \beta x(1-x) - \gamma x(1-x) - (1-x)^2)}{[\dots]} \quad (5.14)$$

At the point where $x = 0$, we can derive from the formula that the difference between $x^+ - x$ is zero. At $x = 1$, the difference between $x^+ - x$ is also zero. This is logical because either the species itself is extinct (at x is 0) or its competitor is extinct (at x is 1) so a change in frequency can no longer occur.

To determine the sign of the frequency development near $x = 0$ and $x = 1$, we consider $f(x)$ without $x A_{22}$ because $x A_{22}$ is always positive by definition. If the sign is positive near $x = 0$, it means the species is able to invade a population consisting of the competitor. If the sign is negative near $x = 1$, it means a population of the species can be invaded by a competitor.

$$f(x) = \alpha x - \alpha x^2 + \beta(1-x) - \beta x(1-x) - \gamma x(1-x) - (1-x)^2 \quad (5.15)$$

$$f(x) = \alpha x(1-x) + \beta(1-x) - \beta x(1-x) - \gamma x(1-x) - (1-x)^2 \quad (5.16)$$

$$f(x) = (1-x)(\alpha x + \beta - \beta x - \gamma x - 1 + x) \quad (5.17)$$

Near $x = 0$, the sign of $x^+ - x$ will be positive if

$$\alpha x + \beta - \beta x - \gamma x - 1 + x > 0 \quad \text{and thus} \quad \beta - 1 > 0 \quad (5.18)$$

Near $x = 1$, the sign of $x^+ - x$ will be negative if

$$\alpha x + \beta - \beta x - \gamma x - 1 + x < 0 \quad \text{and thus} \quad \alpha - \gamma < 0 \quad (5.19)$$

Of course, following the same reasoning, near $x = 0$ the sign of $x^+ - x$ will be negative if

$$\beta - 1 < 0 \quad (5.20)$$

and near $x = 1$, the sign of $x^+ - x$ will be positive if

$$\alpha - \gamma > 0 \quad (5.21)$$

With the behaviour of the formula known, we can derive what the conditions are in pairwise competition for either S_1 to win, S_2 to win, get a stable or unstable equilibrium.

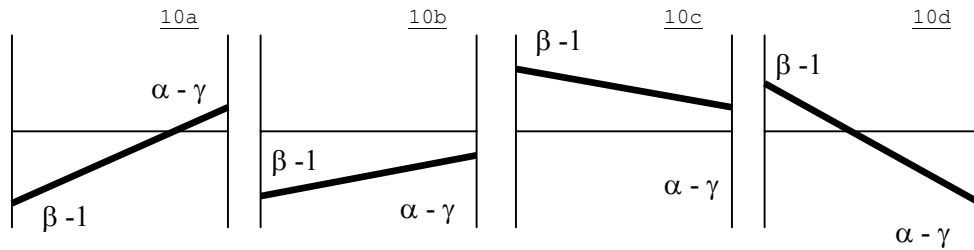


Figure 10. Conditions for coexistence. From left to right in each graph: frequency of S_1 (' x ' in formula 5.20 and 5.21) from 0 to 1. In a, both species can invade a resident population and end up in stable coexistence. In b, S_1 can invade and become dominant. In c, a S_1 can not invade and the resident stays dominant. In d, both S_1 and S_2 can invade and become dominant, depending on start frequencies. For calculation of the parameters, see Formula 5.18 to 5.21.

On the basis of formula 5.18 to 5.21 and the seed mass outputs in the pay-off matrices for competing types, we can predict for each competing species pair if for a species invasion is possible or if it goes towards extinction.

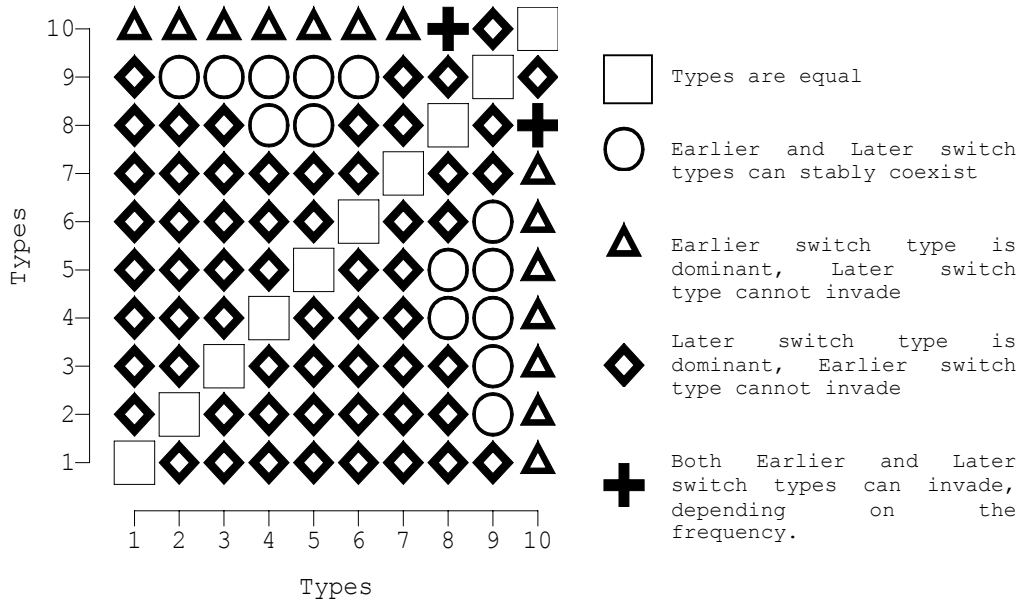


Figure 11. Invasion plot for TBS strategy types. Depicted are the invasion and coexistence possibilities per system of two species. For a description of types, see Table 2.

We have to note, however, that in the game-theoretic simulations performed and reported in this chapter, invasions occurred into communities of variable composition instead of a population of a single species. Invasion possibilities for those circumstances are much more complex and will not be treated.

**EFFECTS OF DISPERSAL DISTANCE
ON THE COEXISTENCE OF PLANTS DIFFERING IN COMPETITIVE STRENGTH**

Summary

By means of a mechanistic model, we studied the effect of dispersal distance on the performance of annual plant types, differing in competitive strength. The differences in competitive strength originated from a trade-off in investment in vegetative growth and reproduction. With equal competitive strengths, a plant type that dispersed its seed over a short-distance (e.g. locally) was at the disadvantage in colonising ability as well as performance compared to a plant type that dispersed its seed over a wider range (e.g. globally). This originated from a higher competition (and thus lower fitness) within formed aggregates for types with local dispersal. Within a growing season, aggregation was beneficial for the performance of weak competitors when competing with strong competitors. Nevertheless, the detrimental effect of competitive pressure of the strong competitors on the weak competitors was a more important determinant for the population development eventually. The weak competitor actually benefited from a more global dispersal, to enable it to colonise empty patches. Very competitive plants had such a low equilibrium abundance that empty patches naturally developed. When types were allowed to evolve, all types evolved to a very competitive type. Without additional disturbance, a stable coexistence between several competitors, differing in competitive strength, was achieved. When plants dispersed their seed over short distances, possibilities for coexistence were reduced. We argue that, in a homogeneous environment with local density and frequency dependent processes, local dispersal will be more detrimental for types of all competitive strengths than found in other studies so far.

Keywords: spatial, plant growth, trade-off, fecundity, competition, dispersal distance, evolution, density, carrying capacity

Introduction

Since long, ecologists have tried to solve the paradox of diversity. It has been a much sought after theme ever since Gause (1934) formulated the competitive exclusion principle. This principle stated that no more types could coexist than there are limiting resources. This theory has its roots in the Lotka-Volterra competition equations (Law & Dieckmann, 2000). These equations assume mean field population dynamics at equilibrium densities (Lotka, 1925; Volterra, 1928). Plants, however, with their sessile life-style, have only a limited area in which they interact with other neighbouring plants. Therefore, locally, individuals do not experience mean field conditions (Harper, 1977). Frequently, the inclusion of local dynamics is omitted (Ronce et al., 2000) even though these local conditions could play a mayor role in determining community processes such as population growth (Law et al., 2003).

Differences in local conditions spring from spatial patterns. Spatial patterns will arise in every population where frequency and density dependent processes occur and dispersal takes place (Bolker & Pacala, 1997) even without underlying heterogeneity (Klausmeier, 1999). In turn, spatial processes are crucial for determining structure and dynamics of populations and communities (Nathan, 2000). Possibly, ecological models incorporating the spatial structure of communities demonstrate coexistence of types more easily than models on a non-spatial basis (Cohen & Levin, 1991; Ludwig & Levin, 1991; Durrett & Levin, 1998; Molofsky et al., 1999; Chesson, 2000; Law & Dieckmann, 2000; Murrel et al., 2001).

The mono-specific aggregation of individuals is one of the most studied patterns of all because it is a common feature in many natural plant communities (Silvertown et al., 1992; Rees et al., 1996; Falster et al., 2001). Local dispersal plays a vital role in promoting mono-specific aggregation in homogeneous environments (Herben et al., 1995), although competition is of influence as well (Turnbull et al., 1999; Goreaud et al., 2002). The spatial aggregation of individuals could play an important role in community development (Coomes et al., 2002). Presumably, it reduces the role of inter- versus mono-specific competition. Weak competitors have higher performance with mono-specific aggregation compared to random mixing. In contrast, superior competitors have a lower performance (Stoll & Prati, 2001). In different model simulations, it was found that aggregation delayed (Silvertown et al., 1992; Yu & Wilson, 2001; Rejmanek, 2002) or delayed and even prevented exclusion of a weak competitor by a stronger competitor (Sole et al., 1992; Pacala & Tilman, 1994; Grist, 1999; Goreaud et al., 2002; Higgins & Cain, 2002). Given the results of these studies, it is generally accepted that clustering could promote the coexistence between weak and strong competitors. In addition, an aggregated distribution can increase the space available for inferior competitors (Geritz, 1995; Higgins & Cain, 2002)

Not all studies however find a beneficial effect of clustering on coexistence, even if the advantageous effect of clustering for weak competitors is present (Schmid & Harper, 1985; Pacala & Silander, 1990; Bolker & Pacala 1999; Falster et al., 2001). Several authors claim that the benefits of clustering are only transient (Damgaard, 1998;

Yu & Wilson, 2001). The effect of clustering on the coexistence of species, in models and in natural systems remains elusive as yet (Coomes et al., 2002). It is even argued that aggregation could promote the exclusion of types (Bolker & Pacala, 1997; Chesson & Neuhauser, 2002). If mono-specific densities and thus competition become severe, this could surpass the detrimental effects of inter-specific competition.

In addition to the controversy on the effect of local dispersal and resulting clustering on coexistence of life-history types, there is the colonisation/competition hypothesis, as first formulated by Levins & Culver (1971). The theory hypothesises that weak competitors benefit from superior colonisation ability by reaching favourable sites before stronger competitors with lower colonisation ability (Geritz, 1995; Huxel & Hastings, 1998). Accordingly, weak competitors with high colonisation ability can coexist with superior competitors. This could be an important mechanism of coexistence in annual systems (Rees et al., 1996). Usually, colonisation ability is regarded as dispersal distance or, more often, a combination of dispersal distance and fecundity. Tilman (1994) found in his model that an unlimited amount of types could coexist based on this trade-off.

There exists a discrepancy between both theories. Is it better for a weak competitor to disperse locally and aggregate to reduce inter-specific interactions, or disperse globally and have a better chance of reaching favourable sites? Is there an effect of dispersal distance on the coexistence per se? In this chapter, we try to elucidate the effect of dispersal distance and the resulting patterns on coexistence by taking explicitly into account the growth and competition of individual plants. Realistic plant interactions are essential for understanding the process of pattern formation in a community. Most studies assume linear competition functions or some competition and colonisation hierarchy, along with unrealistic assumptions of instantaneous replacements of individuals (Pacala & Rees, 1998; Grist 1999). In our model, growth and development of individuals is on a mechanistic basis. The simulated communities are self-assembling; no community processes are presupposed. In addition, externally induced disturbances are not included. All patterns and dynamics spring from the plants in the community itself. This is a difference with traditional competition/colonisation theory where regular disturbances or regular mortality dictate the conditions for coexistence. Seed set is dependent on the reproductive strategy of the plant, and the competitive effects of the number and type of neighbouring plants. This study is one of few that explicitly take the local density and frequency into account.

The goal of this chapter is to study the effect of dispersal distance on performance of weak and strong competitors. Differences in competitive strengths between types originate from a trade-off in the investment in either vegetative growth or generative output. Investigated first is the influence of dispersal distance on the population development of types in monocultures. Next, the effect of dispersal distance when competing types are of equal competitive strength is investigated. Furthermore, we study the effect of dispersal distance on the possibilities of coexistence of types with different competitive strengths. We monitor the population development and pattern formation of all types during population growth, and at equilibrium.

Methods

We assume a limited-sized environment, which is divided into sub-cells of similar size. Within the separate cells, the leaves of individual plants are completely mixed. To calculate the performance and fitness of individuals within cells that contain a different composition of plant types, we use a mechanistic model. Plants grow for a period of 365 days and consequently die. During the growing season there is a constant horizontal light supply from above the vegetation. Within the vegetation, the vertical light climate is determined by the interception of light by the leaf area of plants. It is assumed in this model that light is single limiting resource for the plants. Individual plants grow according to a strict carbon balance. Per plant, photosynthetic production is calculated based on the light climate in the resident cell, the amount of leaf area and the vertical distribution of the leaf area. Every plant has to maintain its structural mass. A part of photosynthetic production therefore goes to maintenance costs. The remaining photosynthetic product is then allocated to the different plant parts. Carbon is allocated first to height growth, then to leaf and root growth. If the plant is in reproductive mode, a fixed percentage of net photosynthetic production is allocated to seed mass production before allocation to vegetative structures. The allocation pattern is specific per type. If plants have large costs that cannot be accounted for by net photosynthetic production, they will shed leaves and root and use the retractable carbon within these structures to account for the costs. If an individual has no root mass or leaf area left, it is considered dead. For a more detailed description of this mechanistic model, we refer to Chapter 2.

Per plant, the amount of produced seeds is calculated from the total of produced seed mass at the end of the simulation period. Seeds have a fixed size of 0.2 gram. The number of individuals of a type in a successive simulation year is based on the total number of seeds produced by that type in the preceding year. Seeds are distributed in the environment. Distribution of produced seeds per plant is based on a Gaussian distribution.

$$\text{Gaussian Distribution} \quad P(x) = \frac{1}{\sqrt{2\pi\sigma^2}} \cdot e^{-\frac{(x-\mu)^2}{2\sigma^2}} \quad (6.1)$$

Here $P(x)$ is the chance that a seed is dispersed a certain distance, σ^2 is the variance, μ is the mean dispersal distance. Adjusting the variance of the Gaussian distribution can vary the dispersal distance of seeds. We distinguish dispersal with a variance of 3 cm ('local dispersal') and 30 cm ('global dispersal') respectively. The mean of the distribution is always zero centimetres. When seed is distributed, the density per cell is dependent on the seed produced by the various plants and their distance to the cell. All plants are assumed to disperse from the centre of the resident cell. If seeds disperse further than half the length of the cell in either the x or y direction, they are assumed to have landed in a cell other than the resident cell. As an example, if the cells are ten by ten centimetres, a seed that disperses within five centimetres in both the x and y direction will fall in the resident cell. All produced seeds are assumed to germinate and grow. The performance of the

plants depends on the density and type of neighbours in the cell. Within cells, composition can differ in terms of both the frequencies of types and densities. For an example of the distribution distances of 250 random seeds with local dispersal see Figure 1.

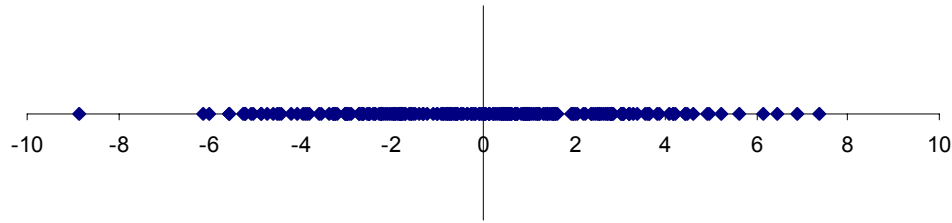


Figure 1. The simulated dispersal distance of 250 seeds, distributed with a Gaussian dispersal kernel. The dispersal distance is given in centimetres. The mean of the distribution is zero centimetres. The standard deviation is three centimetres.

In a real situation, seeds may have a longer dispersal distance owing to additional structures like plumes or hooks (Soons & Heil, 2002). The necessary extra investment will reflect in the carbon left for construction for the actual seeds (Cohen & Motro, 1989; Sakai et al., 1998). Either the number of seeds will be less, or the average weight of the seeds. This would put a cost on long distance dispersal for the type, making it less attractive for a plant to disperse far. In this chapter, we want to assess the influence of dispersal distance *per se*. We assume the dispersal distance as a given trait, and investigate what influence it has on the performance of types. In this way we can assess the benefits and costs for dispersal for plants in different situations and with different competitive strengths. Therefore, we do not take into account any additional costs for long dispersal.

We perform all calculations for types of two different strategies (see Table 1) each with their own allocation pattern. Cohen (1971) and Iwasa (2000) showed that the optimal strategy for plants in terms of reproductive output is to first invest all photosynthetic production in vegetative mass, and subsequently make a clear switch to investments in reproduction. However, a clear switch is not readily observed in plants. Most plants show a gradual transition to reproduction, and some plants show a prolonged investment in both vegetative and generative structures (Rathcke & Lacey, 1985). This can be caused either by environmental factors, like an unpredictable environment that makes early (partial) investment beneficial (Zeide, 1977) or an impossibility to divert allocation pathways instantaneously (Iwasa, 2000). In these plants, investment in reproduction directly interferes with vegetative growth. In this study, we consider types of both life-history strategies. The first is the Seed Portion Investment (SPI) strategy, in which a constant proportion of carbon from net photosynthetic production used for the production of seed. The remaining part is invested in vegetative growth. Types within this

strategy differ in the portion of net photosynthetic production allocated to seed production. See Table 1 for distinguished types. Secondly, we consider the Time Based Switch (TBS) strategy. Types of this strategy invest all net photosynthetic production in vegetative growth at first, but switch to divert all net photosynthetic production to seed at a certain point in time. Types within this strategy are distinguished by their exact timing of the switch to seed production. See Table 1 for distinguished types.

Table 1. Different types within the Seed Portion Investment (SPI) and Time Based Switch (TBS) Strategies. Types within the SPI strategy constantly invest a given portion of net photosynthetic production in seed mass. Types within the TBS strategy invest all net photosynthetic production in seed mass from a given switch date onwards.

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7	Type 8	Type 9	Type 10
SPI (Portion of NPP)	1.0	0.9	0.8	0.7	0.6	0.5	0.4	0.3	0.2	0.1
TBS (Days to switch)	5	25	45	65	85	105	125	145	165	185

Plants of all types have identical height and leaf area size at the start of growth (see Table 4 in Chapter 3). The differences in allocation pattern cause variance in competitive strength during plant development. For the SPI types, the plants that continuously invest a lot of carbon for the production of seed mass, invest little in vegetative mass and consequently are less competitive during a lifetime. Competitive strength ranges from SPI type 1, which is the weakest type, to SPI type 10, which is the strongest type. For the TBS types, the types that start investing all net photosynthetic production in seed at an early point in time have a short period for vegetative growth and are competitively weak. Competitive strength ranges from TBS type 1, which is the weakest type, to TBS type 10, which is the strongest type.

Results

The influence of mono-specific density on seed set

Generally, in crowded situations, plants receive less light and seed production per individual therefore is less. The sum of seed production of all individuals together, however, may exceed the seed production of lower densities. This is an important feature for fitness of the type at different densities.

We will assess the seed production for individuals of a single type at different densities. This will help interpret the performance of types in various circumstances in the coming simulations.

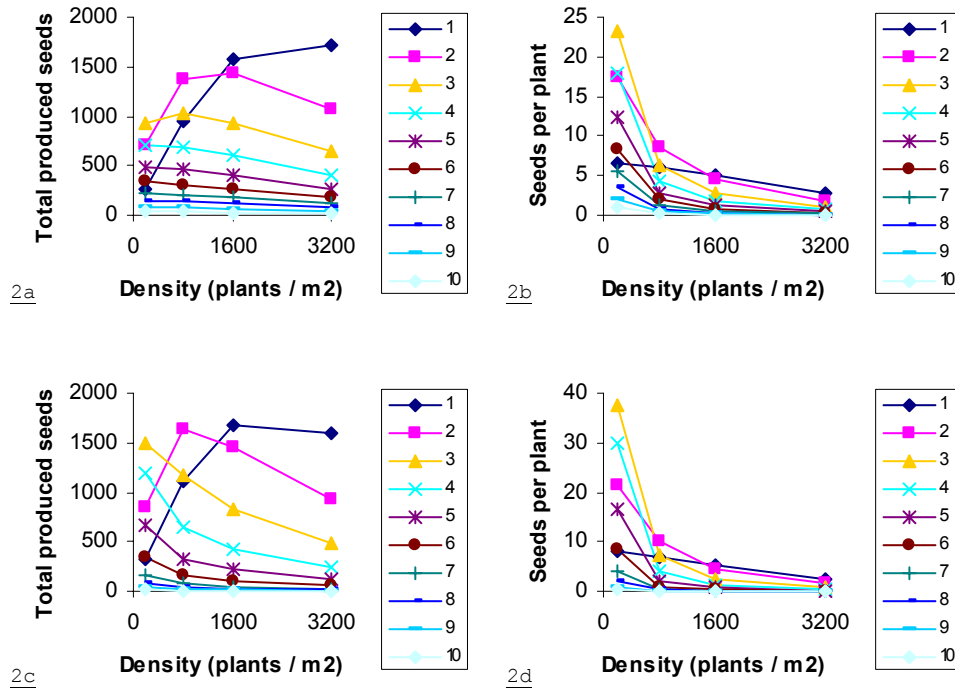


Figure 2. Seed production at different densities. a and b depict the seed production for SPI types, c and d depict the seed production for TBS types. The left graphs (a and c) are the total produced seed per type per density. The right graphs (b and d) depict the produced seeds per plant per type. See Table 1 for a description of types.

In both SPI and TBS types, the total seed production for low competitive types first increases with density before it declines (Weiner, 1988). For types of higher competitive strength, increased densities cause a lower overall seed production. The seed production per plant decreases with density for every type (Weiner, 1982, Pacala & Silander, 1985). The types that are intermediate in competitive strength have the highest seed production per plant at low densities. At higher densities, however, seed production per plant reduces rapidly. In types with lower competitive strength, the reduction in produced seed per plant is less.

The carrying capacity

There is a limit to the number of individuals able to grow and reproduce in a certain sized environment. At low density, individual plants will on average produce more than one seed. At the density where individual plants on average produce one seed, population density is stable. The density thus determines the steady state seed production and size of

the plants. If types are assumed to form mono-specific aggregates, this equilibrium density will determine the invasion probabilities for other types.

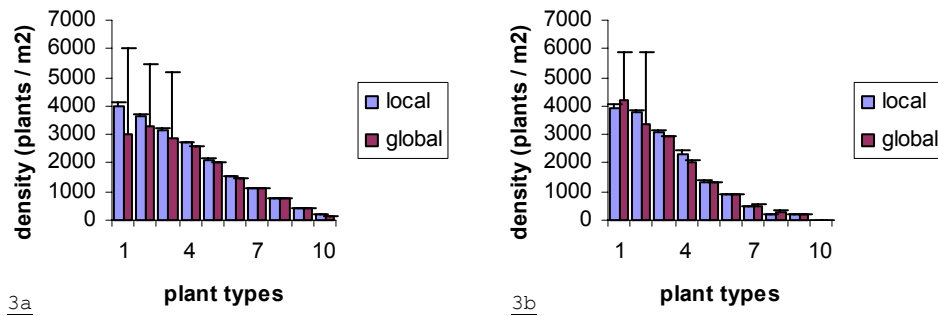


Figure 3. Average equilibrium densities (individuals per m²) during 12 years of equilibrium. Equilibrium was assumed when, at visual inspection, densities of types did not show a visible trend. Depicted in the figures are SPI types (a) and TBS types (b), when distributed locally and globally respectively. For a description of types, see table 1.

In Figure 3 can be seen that there is a profound difference in carrying capacity of the environment for the different types. Generally, the environment has the highest carrying capacity for competitively weak types (see also Coomes et al., 2002). Because of their small stature, competitive pressure is less for weak competitors. The population can grow to high densities before seed production is affected.

The kind of dispersal (local or global) influences the stability of the carrying capacity at equilibrium density. The weak competitors show fluctuations in density, causing a high deviation from average equilibrium density from year to year. This is because these types show an overproduction of seeds at lower densities, causing mass extinction in the next year. Every time the population size drops to a low level, there is a possibility of extinction for these types. Although we do not show the data here, the weak competitive types went extinct frequently in performed simulations. Types that disperse locally have a more stable equilibrium. This is because locally dispersed individuals form aggregates. The plants have high densities within aggregates and lower density towards the edges of aggregates (see Figure 4). Within the centre of the aggregate, competitive pressure is high and seed production is low. At the same time, the individuals on the edges can produce many seeds. In the next year the individuals in the former centre of the aggregate have high seed production because of low density. Because of the aggregates, a portion of the population is always able to produce seed.

The mode of dispersal also affects the carrying capacity itself. On average at equilibrium density, individuals with global dispersal produce slightly less seeds than individuals with local dispersal. This can also be explained with the help of Figure 4. In

this figure, it can be observed that the density distribution of TBS type 4 with local dispersal is over a much broader range than the density distribution with global dispersal. Individuals at the high end of the density range will not produce seeds. All individuals at the beginning of the range will produce a disproportionate amount of seed, causing a continuously high abundance of plants at equilibrium density. Yu & Wilson (2001) and also Kadmon (1993) pointed out that a few individuals in patches of favourable conditions might cause the bulk of seed production for a population, even though most individuals are in patches with unfavourable conditions.

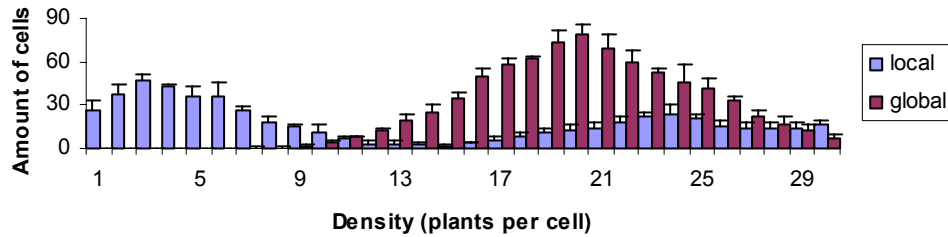


Figure 4. Differences in density distribution at equilibrium of TBS type 4 when dispersed locally (average 3cm) and globally (average 30 cm) in an area of 20 by 20 cells.

The amount of empty patches per area is also of interest, for in these patches any type can establish irrespective of competitive strength. Figure 5 shows the percentages of empty cells at equilibrium densities for SPI and TBS strategies, per type.

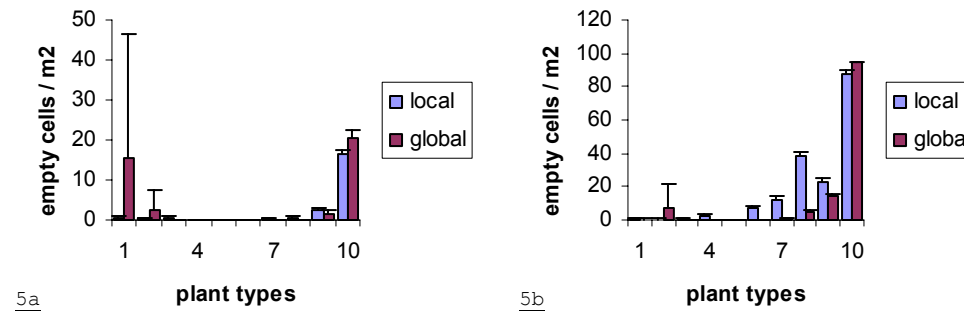


Figure 5. Average number of empty cells per m^2 for populations 12 year at equilibrium density. Depicted are the empty cells for populations of SPI types (a) and TBS types (b), when distributed locally or globally respectively.

Within both strategies, the extremely weak and strong types have the highest percentage of empty patches. Strong types have a high percentage of empty patches because of their low density at equilibrium (see Figure 3). In weak types, density varies greatly from year to year even though the population on average is at equilibrium density (see Figure 3). This is especially the case with global dispersal. In accordance, the percentage of empty patches varies per year in weak types, causing a high standard deviation.

With regard to dispersal distance, it can be concluded that, especially for weak types that tend to an overproduction of seed, the most secure strategy is to distribute seeds locally. With this type of dispersal, types have a lower probability of extinction and can attain a slightly higher equilibrium density than with global dispersal.

Single species performance with varying dispersal distances

In the investigations on carrying capacity in the previous section, a local dispersal caused a more stable and slightly higher population density at equilibrium. It is, however, not necessarily true that this is also the evolutionary stable dispersal distance in a competitive situation. To test this, we take a type and let it develop in a situation with similar types, but with different dispersal distances. It is assumed here that there is no trade-off in the ability to disperse a certain distance and traits like seed number or size. In other words, there is no difference between types, other than the dispersal distance.

For a type of medium competitive ability (type 5) the population developments with different dispersal distances is simulated. The simulations are performed for both the SPI and TBS strategy type. Initial densities are taken low at five individuals per square meter. The population development of local and global dispersing types is simulated for 30 years.

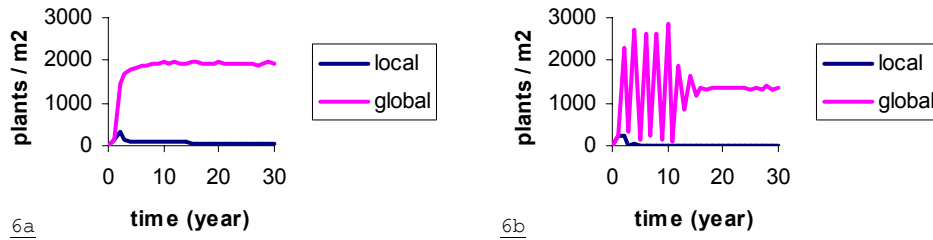


Figure 6. Population developments of SPI (a) and TBS (b) type 5 with either local or global dispersal. Initial densities are 5 plants per square meter. For a description of types, see table 1.

Figures 6a and b show that, although the initial densities for the two types are equally low, the type with local dispersal does not gain a higher abundance, whilst the global disperser increases in abundance rapidly. As could be expected, the local disperser has low

colonisation ability. This has a twofold reason. The first reason is that the dispersal distance is short, and the rate of spread is low. The global disperser can colonise empty cells first. The second reason is that the competitive pressure within clusters is a cause for low seed production, so there are fewer seeds to colonise new spots. Because the global disperser type has lower average competitive pressure during the population development, it can produce more seeds than the local dispersing type. Once the globally dispersing type has established, it cannot be out competed because (presumably) there is no competitive advantage for both the local or the global disperser. In short, a global dispersal distance is a great advantage for rapid colonisation of a site with a low initial density.

At equilibrium density for type 5, all sites are filled (see Figure 5). The colonising advantage of the global disperser to colonise empty sites should be reduced to zero. If the two disperser-types are initiated at equilibrium density, a balance should develop because neither can outcompete the other. In Figure 7 are the population developments of SPI and TBS type 5 with local and global dispersal, when initiated at equilibrium densities.

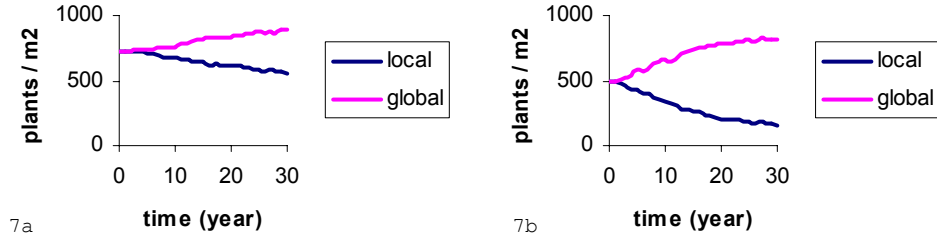


Figure 7. Population developments of SPI (a) and TBS (b) type 5 with local and global dispersal. Initial densities are at equilibrium value. For a description of types, see table 1.

Figure 7 shows that the population density of the local disperser steadily declines. Apparently, the advantage of the global disperser in the previous simulation cannot be attributed completely to a rapid colonisation ability of empty sites. The local disperser apparently has an intrinsic disadvantage when compared to the global disperser. In a monoculture situation, the local disperser had a slightly higher equilibrium density than the global disperser. This was caused by favourable conditions at the edges of aggregates for the local disperser. Individuals at the centre of the aggregate died out, thereby creating favourable sites for the next growing season. In the situation in this section, the locally dispersing individuals experience the density caused by the individuals of the global disperser at the edges of aggregates. An individual local disperser can therefore produce at most the same amount of seeds as individuals of the global disperser, but only at the edges of aggregates. As a result, it produces less seed in total.

It can be concluded that, when plants of different dispersal abilities compete, a local dispersal distance is a disadvantage both during population development and at equilibrium densities. The evolutionary stable dispersal distance will be a more global dispersal distance.

The influence of spatial patterns on performance of types

In a situation of equal competitive strength, types with global dispersal developed a higher population size than types with local dispersal. In a situation where types of different competitive strength compete, this could be different. In an aggregated situation, inter-specific interactions are reduced and mono-specific interactions are enhanced. A weak competitor may benefit from a local dispersal to form clusters, to avoid competition from the strong competitor (Sole et al., 1992; Pacala & Tilman, 1994; Grist, 1999; Goreaud et al., 2002; Higgins & Cain, 2002). According to theory, clustering will be beneficial for weak competitors and detrimental for strong competitors.

We will check this hypothesis by comparing the seed production of weak and strong competitors in an aggregated and a random distribution. For both the SPI and the TBS strategy, we take a range of weak to strong types, as described in Table 1. An area comprised of 40 by 40 cells (16 m²) is initialised by randomly placing 20 individuals of each of the types in the area. We let this system develop for 4 years and assume local dispersal. In 4 years time all species have the opportunity to form aggregates, and the simulation is short enough to ensure that no types go extinct as a result of competitive exclusion. The amount of individuals per type after four years is counted. An equal amount of individuals per type is then distributed randomly in an area of the same size, by means of a random number generator. For each individual, this random number generator randomly picks an x and y coordinate. The produced seed per type after growing a year in the aggregated situation is compared with the situation where plants have grown for a year in the randomly distributed situation. This is depicted in figure 8.

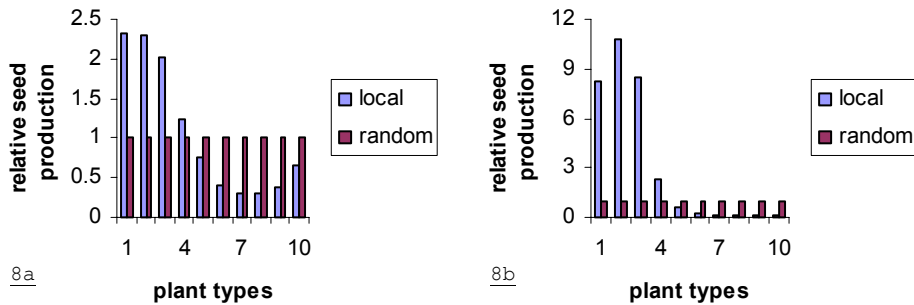


Figure 8. Seed mass, produced from an aggregated setting, relative to seed mass produced in a random setting. Depicted is the seed production of SPI types (a) and the seed production of TBS types (b). See Table 1 for a description of types.

From Figure 8 it is clear that indeed relatively weak competitors benefit from an aggregated situation while relatively strong competitors are subdued, compared to the random situation.

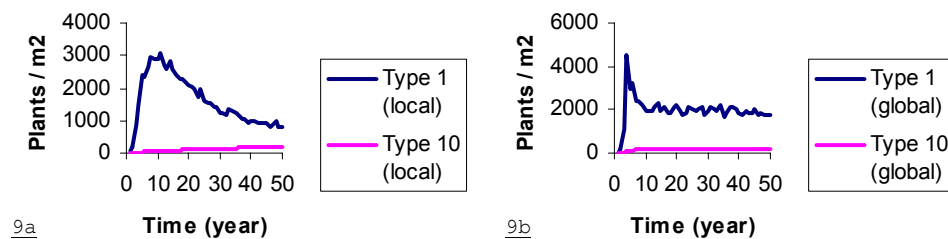
Given that strong competitors have a higher seed mass production when competing with weak competitors, the seed mass production of weak and strong competitors can be expected to be increasingly similar with a local dispersal. However, this does not necessarily mean that coexistence is readily achieved. Effects may be only transient. In the next section, we will investigate whether dispersal distance has an actual effect on the coexistence of weak and strong types during several years.

The influence of dispersal distance on coexistence of strong and weak competitors

In the previous section, it was concluded that a local dispersal is beneficial for the performance of weak competitors when competing with stronger competitors, because of aggregation. This could either enhance coexistence on the long term or merely be a transient effect. To test this, we use a simpler system without so many interacting types.

We assume a weak competitor and a strong competitor, and simulate population development with different combinations of dispersal distances. As a consequence of the allocation strategies of weak and strong types, types differ in fecundity and equilibrium density (see Figure 2 and 3). This gives an opportunity to test the colonisation competition theorem with this system at the same time. In the colonisation competition theorem, a weak competitor can coexist with a strong competitor, given that the weak competitor has superior colonisation ability to reach favourable sites. We investigate whether this superior colonisation ability stems from superiority in dispersal distance or simply from a higher number of seeds. We evaluate steady state population density of the competing weak and the strong competitor in all combinations of dispersal distances: both global or both local, one local and the other global.

First, the SPI strategy types are studied. We start with the most likely combination according to the colonisation /competition theorem: an extremely weak type (type 1) and an extremely strong type (type 10). See Table 1 for a description of these types.



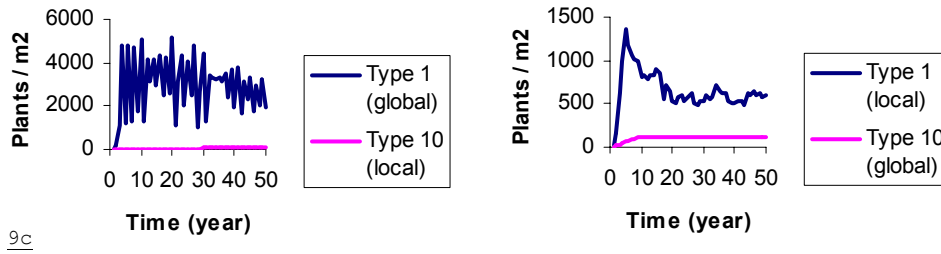


Figure 9. Population developments of competing SPI types 1 and 10. The dispersal mode (global or local) is given between brackets. See Table 1 for a description of types.

The equilibrium densities of the types in the different combinations of dispersal distance are summarised in Table 3.

Table 3. Average equilibrium densities for 10 years at equilibrium (printed in bold) and standard deviations (in parenthesis) for SI types 1 and 10, with either local or global dispersal. For population development, see Figure 9. For a description of types, see Table 1.

	Type 1 local Type 10 local	Type 1 global Type 10 local	Type 1 local Type 10 global	Type 1 global Type 10 global
SPI 1	898 (78)	2610 (768)	578 (50)	1828 (103)
SPI 10	166 (5)	82 (7)	117 (2)	162 (4)

For SPI types 1 and 10, coexistence is possible in all four possible combinations of dispersal distances. For this combination, the dispersal distance is not the determining factor for coexistence. Nevertheless, the performance of the types in terms of population density varies with dispersal distance. At low population density, a type will more easily go extinct. The variation in density may tip the balance if, for any reason, conditions are less favourable for the weaker type. The weak competitor with a global dispersal distance generally achieves the highest population density. The strong competitor performs best, on average, with global dispersal distance too. When the strong competitor disperses locally and the weak competitor disperses globally, the population density of weak type fluctuates strongly around the equilibrium density because of overproduction of seeds.

This is because the strong type leaves more empty spots dispersing locally than when dispersing globally, creating better conditions for the weak type.

Below in Table 4 are the population densities at equilibrium of a less contrasting pair of types: SPI type 7 and 10. These types don't differ much in terms of fecundity. Type 10 invests a portion of 0.1, and type 7 invests a portion of 0.4 of net photosynthetic production in seed.

Table 4. Average equilibrium densities for 10 years at equilibrium (printed in bold) and standard deviations (in parenthesis) for SPI types 7 and 10, with different local and global dispersal. Total simulation time was 50 years. For a description of types, see Table 1.

	Type 7 local Type 10 local	Type 7 local Type 10 global	Type 7 global Type 10 local	Type 7 global Type 10 global
SPI 7	79 (8)	8 (3)	263 (18)	284 (16)
SPI 10	121 (3)	118 (3)	120 (3)	119 (3)

Table 4 shows that these types can also coexist. What can be concluded from these simulations is that a trade-off between seed number and competitive ability does not necessarily need to be strong. Less contrasting types can coexist just as well as very contrasting types, be it at lower densities.

Instead of making the weaker type less weak, the stronger type can also be made less competitive. For the simulation we take a type 1 and a type 8, which is slightly less competitive than the strong type used in the previous simulations. This type 8 has a higher equilibrium density and has a very low percentage of empty cells at equilibrium (See Figure 5). When the combination of type 1 and 8 is simulated, coexistence is not possible (results are not shown).

It seems that the number of plants at equilibrium density, and in particular the amount of empty patches left by the superior competitor, is the most important feature for coexistence in our simulations. The dispersal distance or the fecundity per plant of the inferior type is of lesser importance, in contrast to what most studies assume (e.g. Matsinos & Troumbis, 2002). Higgins & Cain (2002) presumed that spatial and temporal refuges promoted coexistence, rather than dispersal abilities. An inferior competitor with a high reproductive rate and carrying capacity can exploit these refuges. The same phenomenon is found here in this study, be it that in our study, types of a large range of fecundity and carrying capacity can coexist with a strong competitor.

In the previous section, it was shown that, within a year, an aggregated distribution was beneficial for weak competitors and a random distribution was beneficial for strong competitors. From the simulations above it can be derived that this effect is

only transient. When both types disperse locally, the population density of the weak type indeed decreases more slowly. Nevertheless, it can be observed in Figure 9 that population densities do not exceed those with global dispersal at any point in the population development (note that the y-axes are scaled differently in Figure 9). When both types disperse globally, dynamics are faster. It can be concluded that the dynamics resulting from competitive pressures over the years are far more important for the community development than a partial release of competitive pressure within a simulation year.

Next, we carry out simulations for TBS types, differing in competitive strength. These types have a different allocation strategy, in which they switch to seed production at a certain moment in time. Depicted in Figure 10 are the population developments of a competing weak TBS type (type 2) and strong TBS type (type 9) with different dispersal distances. We take these types because of their resemblance to the SPI types 10 and 1 of the previous simulations, in terms of equilibrium densities and empty spots at equilibrium. (Compare SPI types 10 and 1 with TBS types 9 and 2 in Figure 3 and 5).

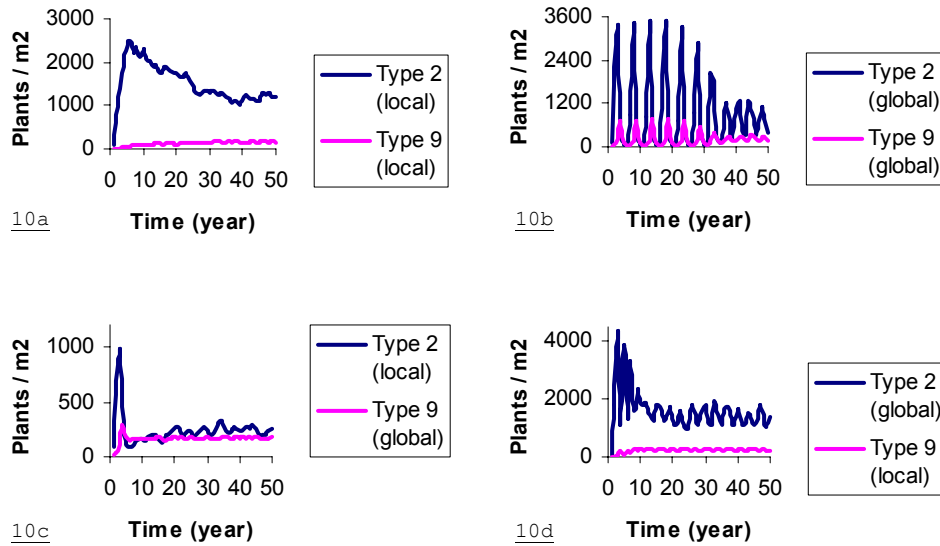


Figure 10. Population developments of competing TBS types. The dispersal mode (global or local) is given between brackets. See table 1 for a description of types.

The equilibrium densities of the types in the different combinations of dispersal distance are summarised in Table 5.

CHAPTER 6

Table 5. Average equilibrium densities for 10 years at equilibrium (printed in bold) and standard deviations (in parenthesis) for TBS types 9 and 2, with local and global dispersal. For population development see Figure 10. For a description of types, see Table 1.

	Type 2 local Type 9 local	Type 2 local Type 9 global	Type 2 global Type 9 local	Type 2 global Type 9 global
TBS 2	1199 (68)	238 (37)	1354 (231)	731 (382)
TBS 9	158 (14)	171 (6)	237 (29)	224 (60)

In TBS types, coexistence also occurs with every combination of dispersal distance when very contrasting types compete. The highest equilibrium population density for the weak type is achieved when the strong type has a local dispersal. Probably, this leaves more empty or low-density spots for the weak competitor to establish and produce seeds. The dispersal distance of the weak competitor is less important, but population densities are lowest when the strong type 9 disperses globally and the weak type 2 disperses locally.

The equilibrium densities of TBS types differing less in competitive strength are summarised in Table 6.

Table 6. Average equilibrium densities for 10 years at equilibrium (printed in bold) and standard deviations (in parenthesis) for TBS types 9 and 6, with local and global dispersal. Total simulation time was 50 years. For a description of types, see Table 1.

	Type 6 local Type 9 local	Type 6 local Type 9 global	Type 6 global Type 9 local	Type 6 global Type 9 global
SPI 6	0 (0)	0 (0)	161 (151)	0 (0)
SPI 9	115 (3)	136 (3)	835 (558)	0 (0)

For the TBS types, a different result is achieved than was the case with SPI types. There is no coexistence between less contrasting types, unless the strongest type disperses locally and the weaker type globally. The amount of empty spots at equilibrium density was about equal for both the strong SPI and TBS types used. If empty spots are the determining factor, coexistence opportunities between slightly contrasting SPI types should be equal to the coexistence opportunities between slightly contrasting TBS types.

The difference lies within the allocation strategy. The strong TBS types wait for a very long period before making a switch to seed production. If they experience low competitive pressures, these types grow so fast that they have almost reached steady state by the time a switch to seed production is made. Consequently, the carbon available for seed production is very low. The plants make very few seeds. In contrast, when some measure of competition is present, the plants are smaller before making the switch to seed. With a small stature, maintenance costs are lower and the strong TBS types have opportunities to make many seeds. Quite counterintuitive, plants that differ less from the strongest type in terms of competitive strength ‘help’ the strongest TBS type to reach a higher equilibrium density, thereby spoiling the opportunities to coexist. Only a type that switches early to seed production attains a stature small enough not to compete with the strong type, and it consequently is able to coexist with the strong type.

Although the SPI and TBS types are comparable in terms of equilibrium density and fecundity in monoculture, the coexistence possibilities between pairs of types of both strategies are different. This shows that it is important to explicitly take into account the mechanics behind plant characteristics, because this may alter results.

Coexistence occurs only in a few very distinct combinations of competing types, namely those including the strongest of all types, SPI type 10 or TBS type 9. In all other combinations of types, the competitively superior type out competes the weaker type. It might be possible, however, that successful combinations of types are more likely to occur than unsuccessful combinations of types. This is investigated in the next section.

A self-assembling community of evolving types

In the previous section we concluded that the coexistence by the colonisation- competition trade-off was not restricted to very contrasting types in the SPI strategy types. Rather, a whole range of different types could coexist with a strong competitor, given that this strong competitor left empty patches in the environment at equilibrium and dispersal was global. Weaker types left no empty patches because of a higher equilibrium density. Consequently, combinations of weaker types were not able to coexist because no empty spots were available for the weakest of both competitors. For the types of the TBS strategy, only the most contrasting types could stably coexist. It can be concluded that generally, of all combinations of types 1 to 10, very few combinations have opportunities to coexist. However, it might be that some combinations of types are more likely to occur than others are and that this will determine the possibilities for coexistence. An important question is therefore which combination is likely to occur.

One method to see which combination of types remains after a period is to simply assume all types can occur simultaneously. To do this, all types would have to be placed in a simulation area at some starting density. After that, competition should be let to take its course until there are no more changes in the composition of the stand. However, some difficulties arise when applying such a crude method. A major problem is tractability. Types will go extinct due to the combined effect of all type characteristics. With so many interacting types, each at different density and frequency, it is hard to

extract the mechanisms or interactions from which types go extinct. A second problem is stochasticity. It is possible that some types go extinct by chance.

Considering these two problems, it probably is more insightful to disentangle the possibilities for coexistence between types and separately investigate the factors causing competitive exclusion. For this reason, we separate some time-scales. This will be explained in the next section. We also introduce evolution of types and random drift. Evolution and random drift are processes that occur frequently in a natural situation. These are important processes to shape communities in their composition.

Via random drift, a type with a certain trait value can arrive in the simulation area, which is comprised of 20 x 20 vegetation cells. Because individual cells are 10 by 10 cm, the total area is 4 m². The newly arrived type is subject to mutations in its trait value. It is assumed that arrival of a type from outside is a rare event and that types have ample time to evolve before a new arrival of a different type. This is the first separation of time scales. The chance for a mutant to develop is set at one mutant in every 1000 individuals per year. The characteristics of the resident type make up the environment for the mutant. This will determine whether a mutant grows in numbers, or goes extinct. If the mutant can grow in numbers, it will have more of an influence on the environment. Possibly, it can exclude the resident type. It is assumed that mutations occur at such a slow rate that a mutant is able to invade in the resident population and establish (or go extinct) before a new mutation occurs. Only if the mutant excludes the original type and the mutant population has grown to equilibrium density, the mutant can mutate once again to a new type. This is the second separation of time scales. In many studies on invading mutants, it is assumed that the evolutionary and population developments time-scales are separate (Law & Morton, 1996; Doebeli & Dieckmann, 2000; Uriarte & Reeve, 2003). The cycle of mutation and exclusion continues to the point where the mutant does not exclude the resident type and both coexist. Every time that a type has mutated and does not mutate anymore (and is 'evolutionary stable') another type can enter the environment via random drift again. See Law & Morton (1996) and Uriarte & Reeve (2003) for a similar study.

For the SPI types, the trait that is subject to mutation is the portion of net photosynthetic production that is invested in seed. The evolutionary step is 0.1. It turns out that, whatever trait value the initial type possesses, evolution always goes towards the strongest types that invests only a portion of 0.1 or 0.2 of net photosynthetic production in seed. Depicted in Figure 11 are the evolving types with either local or global dispersal. In this Figure we have started with the weakest type that invests all net photosynthetic production in seed.

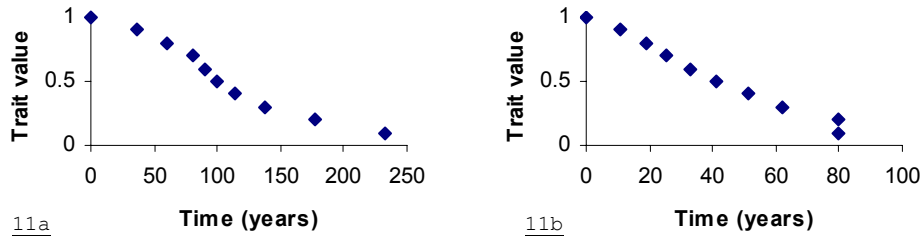


Figure 11. The evolutionary development of SPI type 1. Depicted on the x-axis is the year in which individuals possessing a trait value have excluded all individuals of the previous trait. It is assumed that mutants cannot further evolve until they have excluded all individuals of the former type. SPI types have local dispersal (a) or global dispersal (b). For a description of types, see Table 1.

Figure 11 shows that a locally dispersing SPI type 1 evolves towards a community consisting solely of SPI type 10, the most competitive type. This type cannot mutate back to a less strong type because individual mutants would not survive. A globally dispersing SPI type 1 rapidly evolves toward a community consisting of a mixed population of SPI type 10 and 9. Apparently, type 9 has a better performance with global dispersal than with local dispersal. If we start with an intermediate type in terms of seed investment, it will evolve towards the same types. Both SPI types 9 and 10 are strong competitors with a low equilibrium density (see Figure 3a). This means that there will be empty patches at equilibrium and thus possibilities for coexistence.

To assess which types will coexist, we introduce a new type once again and give it the possibility to evolve, now against a background of a (non-evolving) type 10. We start with globally dispersing types. This results in a coexistence of type 10 with type 9. With this combination of resident types, any newly introduced type evolves to a type 8. Within this combination of resident types, any new type evolves to a type 6. Apparently, mutants of a type 7 are not viable. At this point, with a resident community consisting of type 10, 9, 8, and 6, type 1 and 2 are no longer viable strategies and go extinct quickly when introduced. Type 3 however does not go extinct and is able to mutate to a type 4 in year 275. This new type goes extinct after 300 years after all (see Figure 12). Type 10, 9, 8 and 6 however continue to coexist.

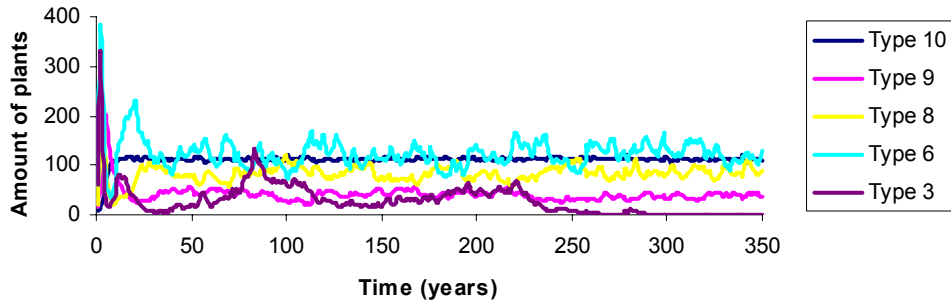


Figure 12. Coexisting SPI types. Types were introduced one at the time, at the point when the types that were already present did not evolve any longer. The figure depicts the situation with resident types 10,9,8 and 6 and introduction of Type 3. This type goes extinct (in year 290) after having evolved to a Type 4 (in year 275). For a description of types, see Table 1.

An interesting notion is that, while the four types 10, 9, 8 and 6 can coexist, individual pairs of these types (e.g. combinations of 9, 8 and 6) are not able to coexist. The strong type 10 suppresses the other types so that their equilibrium abundances continuously stay low. In this way, enough empty patches remain for all of the types to coexist.

When this same set of simulations is done for SPI types with local dispersal, types tend to die out more easily. In a resident population of type 10 plants, a newly introduced type evolves to type 7 and partially to type 8. However, when a new type of lesser competitive ability (like Type 1) is introduced, type 7 and 8 die out. This difference in behaviour of types with global or local dispersal is caused by the different spatial pattern that results from the two dispersal distances. The distribution of locally dispersing types is highly aggregated. These types have a higher chance of encountering conspecifics than based solely on their frequency. Additionally, the density within aggregates is very high, causing a lower overall fitness for the types. While a combination of type 7 or 8 with type 1 would render type 7 or 8 the winner, type 10 keeps the abundance of both 7 and 8 low. Type 1, with its high equilibrium density, can persevere and even outcompete type 7 and 8.

For TBS types, we perform the same analysis. The evolving trait in TBS types is the switch to reproduction. We allow the type to evolve with an evolutionary step of 20 days. In Figure 13 it can be seen that all types evolve to TBS type 9. Thus, the evolutionary stable TBS type is type 9.

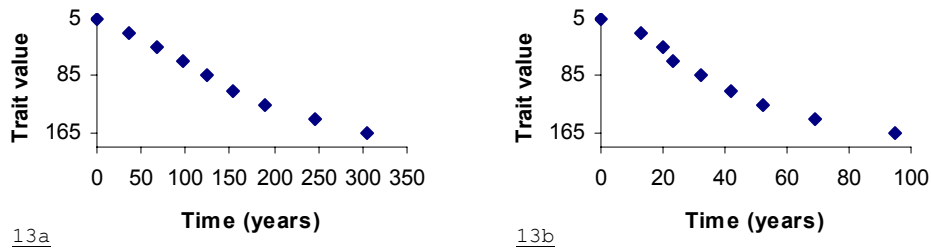


Figure 13. The evolutionary development of TBS type 1. Types with local dispersal (a) or global dispersal (b). Given in the Figure are the evolved trait values, and in what year they have excluded all individuals of the previous trait. It is assumed that mutants can not evolve until they have excluded all individuals of the resident type.

A new weak type (type 1) is assumed to enter the community of type 9 via random drift. The population developments of the new type with global dispersal are depicted in Figure 14.

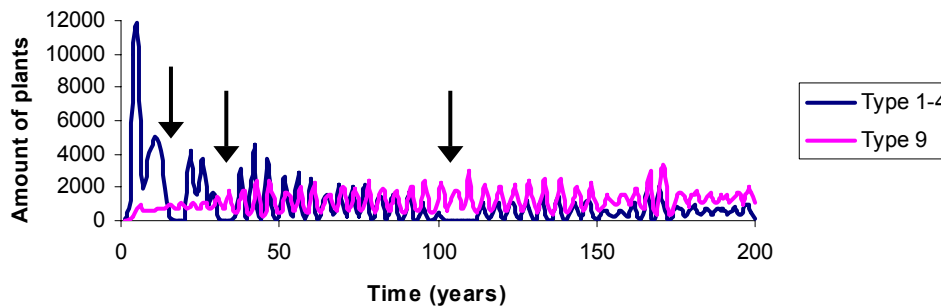


Figure 14. The evolutionary development of TBS type 1 against a background of type 9. Arrows depict the years in which the type have evolved completely to a new timing in the switch to seed production. The final type is type 4. It is assumed that mutants cannot evolve until they have excluded all individuals of the resident type. See Table 1 for a description of types.

The newly introduced type 1 is able to evolve to a type 4, and after that does not evolve any more. As can be seen in Figure 14, the population density is highly variable between years. In a small area, both global dispersing types 9 and 4 have a high chance of extinction. If the simulation is repeated for locally dispersing TBS types, the population development is smooth. The newly introduced type 1 can evolve to a type 3 and no

further. The more competitive TBS types enable the TBS type 9 to gain a higher seed production (see the previous section: ‘The influence of dispersal distance on coexistence of strong and weak competitors’). Therefore, in TBS types, only very contrasting types meet the dual condition of evolutionary stability and no competitive exclusion. If in this new situation yet another type is introduced, it is not viable.

With these simulations, we show a method to assess the evolutionary stability and coexistence possibilities of types differing in competitive strength and fecundity in a traceable way. Dispersal distance was a determining factor for the evolutionary stability of combinations of types.

Discussion

In this study, the focus is on plants that differ in fecundity and competitive ability because of an allocation trade-off. Plants invest their carbon from net photosynthetic production either in reproduction or vegetative growth. The advantage for types investing little in vegetative growth is a relatively high fecundity and a high equilibrium density. Types with high investment in vegetative growth have the advantage that they are competitively strong. We investigated the effects of dispersal distance on the resulting patterns of coexistence between types differing in allocation strategy. An important feature in this study is the simulation of mechanistic growth of plants instead of rule-based simulations or calculations.

Within types of equal competitive strength, it was clear that local dispersal was an unfavourable strategy in the presence of similar types with global dispersal. A type with local dispersal had a lower overall colonisation rate, caused by a smaller dispersal distance and a lower number of seeds caused by the higher competitive pressure that resulted from local crowding. This was, however, not the only cause. Population densities of the locally dispersing type declined rapidly in favour of the globally dispersing type, even if both were initiated at equilibrium densities and no empty cells were present that would give the global disperser a colonisation advantage. From the analysis it can be concluded that, for types of equal competitive strength, local dispersal is not a viable dispersal mode because of local crowding effects. In a modelling study, Ezoe (1998) found that the optimal dispersal distance is always much smaller when the effect of spatial clumping is neglected. Spatial clumping thus is an important factor determining the optimal dispersal distance.

When species of unequal competitive strength competed, local dispersal did have beneficial effects for weak competitive types. Individuals of a weak competitor produced more seed in a single growing season with an aggregated distribution than in a random distribution. As already shown in field experiments (Stoll & Prati, 2001) and many simulation models, this was caused by a reduction of inter-specific competition and simultaneous increase in intra-specific competition in an aggregated situation. Nevertheless, whenever a weak and strong type competed for a longer period of time, the seed production of individuals of the weak type was greatly reduced from year to year by

the competitive pressure of stronger competitors. This was more important for population development than the relative benefit of aggregation within a year. Having local or global dispersal had no influence on the final resulting vegetation composition. Higgins & Cain (2002) also pointed out that aggregates would not alter community development in case of a competitive hierarchy. Within an aggregate, individuals of the weak type will replace other individuals of the weak type and thus will not increase in abundance. At the edges of the aggregate, individuals of the weak type will be excluded, and overall the weak type will decrease in abundance. Pacala & Silander (1990) also argued that aggregation is not fundamental for community dynamics.

The amount of empty patches that the strongest competitor left in the environment at equilibrium density was the main determinant for coexistence of types. In traditional competition/colonisation models, empty patches by disturbance or mortality are a requisite for coexistence but usually not considered the main cause. In those models, coexistence is mostly based on a superior colonisation ability of the weak competitor, although this is not always implemented explicitly. We show here that dispersal distance is not the most important factor to achieve coexistence between types of different competitive strength. Coexistence was possible in most cases if the strong and the weak type both had global dispersal and the strong type left empty patches in the environment at equilibrium density. Local dispersal was detrimental for the weaker type and mostly irrelevant for the stronger type. In addition, the differences in fecundity between a strong and a weak competitor needed not to be extreme to achieve coexistence. Higgins & Cain (2002) also presumed that spatial and temporal refuges promoted coexistence, rather than dispersal abilities. An inferior competitor with a high equilibrium density can exploit refuges. This phenomenon was demonstrated in this study. In combinations of types with slightly lower competitive strength, and thus higher equilibrium densities, the number of empty patches reduced to an extent that coexistence with other types was not possible.

Regarding the fact that only combinations containing the type with low equilibrium density are viable, the possibilities for coexistence between any randomly chosen pair would be small. However, when we allowed single types to evolve with regard to their competitive ability, the type that always evolved was the strongest of all types, with a low equilibrium density. This most competitive type suppressed all other types to such an extent that empty patches remained in the area. This allowed for a combination with weaker types that made use of the empty patches left by the stronger types in the environment. Up to four types could stably coexist. An interesting notion is that individual pairs of these types could not coexist. Law & Morton (1996) in their modelling study also found that some species coexisted only because others (had been) present.

When types dispersed locally, the types also evolved to the strongest type. Newly added types evolved to relatively strong types. These additionally added and evolved types, however, went extinct every time a new type entered the community (Law and Morton, 1996). This shows that the self-organising patterns arising from dispersal distance do profoundly affect community assembly.

For types that base seed production on time passed since emergence, the stable combination was the strongest competitor with a very weak competitor. These types were strongly contrasting in terms of competitive strength and fecundity. The mechanism by which the types could coexist, however, was not related to the competition/colonisation trade-off. The cause was a better performance of strong competitors in the face of strong competition. Once weak competitors evolved towards a stronger type, the strongest competitor could gain a higher equilibrium density, thus spoiling the possibilities for coexistence. This caused that types newly added to the strongest type 9 could evolve to a type 3 but no further. This shows that to understand the possibilities for coexistence it is important to regard the mechanisms behind a competitive hierarchy.

In general, it was shown in our simulations that local dispersal was not beneficial for coexistence of types. In a natural situation, many plants appear to have an aggregated distribution. We can think of several conditions in which local dispersal will be beneficial. If the environment is heterogeneous and consists of permanently favourable and unfavourable patches, there is a high chance of a seed with local dispersal landing within the favourable patch from which it is dispersed (Lavorel et al., 1994). Secondly, there could be costs involved for long distance dispersal, for instance caused by costs of producing dispersal structures (Cohen & Motro, 1989; Sakai et al., 1998). This would reduce the benefits of long distance dispersal, for instance because a lower number of seeds can be formed or the mass per seed decreases. Thirdly, if there is a trade-off between differences in seed size and number, and this is correlated with competitive strength and dispersal ability, an advantage for short dispersal will be possible. This will depend on the advantage of seed size and related competitive strength relative to crowding effects. Lastly, there could be a 'mass effect' of advertisement for pollinators, promoting the clustering of individual plants.

In a more realistic situation, individual plants experience variable overlap of leaf area with neighbouring plants. It is possible that in real systems more small spots exist where a plant of small stature could prosper (Dushoff et al., 2002). In that case, there will be more opportunities for a good disperser with high fecundity to coexist with stronger types. In addition, we do not assume any variation between plants of the same type when situated in a single vegetation cell. In our model, if a great number of plants inhabit the same cell (as occurs with local dispersal), it is possible that none will come to reproduction. In a real situation, small differences between individual plants will cause size hierarchies (Anten & Werger, 1996). This will enable at least one or a few plants to grow to a large size and reproduce. This would make local dispersal less harmful for the performance of plant types. Also, fluctuations like we saw in the equilibrium density of competitively weak species will likely be less when size hierarchies can be formed. Annual plant populations, for instance, are characterised by a smooth approach to an equilibrium point and overcompensation is rare (Rees et al., 1996; Freckleton & Watkinson, 2002). The effect of thinning on results presented in this chapter will be worthwhile to investigate.

Lastly, it should be noted that our results are valid only for annual types. Most likely, perennials will show different behaviour.

THE ROLE OF CROWN SHAPE IN PLANT GROWTH AND COMPETITION

Summary

The vertical distribution of leaves is an important feature that determines light interception for individual plants within vegetation canopies. It is therefore a determinant for competitive strength under light limitation. An experiment was designed to demonstrate an alteration in the vertical distribution of leaves (i.e. a change in crown shape) under competitive pressure. It was found, however, that selected plants did not show any change in the shape of the crown under the different competitive pressures and nutrient availabilities applied the experiment. Plants did show an increase in height when neighbouring plants were taller (and thus light capture was reduced). With help of a mechanistic model, we investigate the restrictions and possibilities for plants to change their crown shape and at the same time grow in height. According to the model results, having leaf area at a high position along the stem, or changing crown shape to achieve this, was beneficial only for competing plants that were slowly growing in height. Having more leaves at high positions became less beneficial when combined with a more rapid growth in height. In competition, a larger height growth improved the competitive strength even where a simultaneous high position of leaves was no longer beneficial. Height growth was thus more important in determining the competitive strength than a change in crown shape. For single isolated plants, model results showed that it was better to change crown shape, irrespective of height growth. A change in shape kept the plant away from a steady state at which no more growth is possible. We hypothesize that during competition, it will be beneficial to keep a relatively low leaf area distribution and invest in height growth. Whenever plants gain a dominant position and the competitive pressure (and height growth) is reduced, it might be beneficial to start redistribution of leaf area to higher positions, as this would keep the plant out of steady state and enable further growth.

Keywords: crown architecture, pipe model, competition, fitness, vertical leaf area distribution

Introduction

Crown architecture determines the position of leaves, the light interception and thus the ability to acquire carbon for future investments (Bongers & Sterck, 1998). In situations where resource availability is changed by neighbouring plants, it will determine competitive success (Tremmel & Bazzaz, 1995). Crown architecture is not constant; it changes during the growing season and also from year to year during growth (Ross et al., 2000). For instance, crown architecture may change with the ontogenetic development of the plant or with age (Kawamura & Takeda, 2002).

Independent of the ontogeny, many species show plasticity in crown architecture as a result of the perceived light climate. Plants detect the light availability as a change in the ratio of red to far red light. A well-known reaction to a low availability of light within a vegetation canopy is the stem elongation response, which many plants exhibit (Weinig, 2000a). For plants growing in dense stands, this reaction enables the plant to place leaves higher in the vegetation canopy, increasing possibilities for light interception. Placing leaf area at positions high along the stem will produce a similar result, because this process also brings more of the leaf area in a favourable position in the light gradient. Simultaneously, plants may cast away heavily shaded leaf area that is positioned low along the stem, relieving the plant of a respiratory burden. Such a change in the vertical distribution of leaf area, henceforth called a change in crown shape, may help plants withstand suppression by neighbours (i.e., competitive response, sensu Goldberg 1990). A change in crown shape could also give a plant an extra competitive advantage over its neighbouring plants, so it can suppress neighbouring plants more efficiently. We would therefore expect plants to change their crown shape when competing for the available light with neighbouring plants. On the other hand, the support of leaf area costs carbon, and these costs increase disproportionately with height. This may limit the plant in the positioning of leaf area along its height (Chazdon, 1986). A positive effect of a change in crown shape may highly depend on the actual light that a plant intercepts, the returns in terms of increased light interception with a better positioning of leaves versus the costs this implies.

In a student's experiment (van Nieuwenhuizen, 1996) it was investigated whether plants would exhibit a change in crown shape when competing within a high or low vegetation canopy. It was hypothesised that plants growing within the high vegetation canopy would show a bigger change in the shape of the crown for these plants would have to compete most with the plants in the surrounding canopy for the available light. A change in crown shape would benefit these plants. The change in crown shape, height and leaf area was monitored in three successive harvests. The competition experiment was carried out with two species with different growth forms, both commonly occurring in the chalk grasslands of Western Europe. *Origanum vulgare* is an herbaceous perennial species, reaching 30-40 cm in height. It has stems and its round leaves are placed along these stems. The other species was *Brachypodium pinnatum*, a perennial grass, reaching 40-50 cm in height. This species has short stems which end in long erected leaves. Single plants were placed within a canopy of either con- or hetero-specifics, at two different

nutrient levels. A more elaborate description of the methods of the experiment is given in Appendix 1.

Surprisingly, the plants did not show any change in crown shape whether in mono or mixed culture, at low or high nutrient availability, or in time with harvests. The plants continuously kept leaf area at low positions along their height (see Figure 7 in Appendix 1). Plants did increase in height when competing within a canopy of the taller of competitors, *Brachypodium pinnatum*, when compared with competition within a canopy of *Origanum vulgare* (see Figure 7 in Appendix 1). It seems that plants do show a plastic response in height growth on the basis of shade. Why plants did not bring more of their leaf area to higher positions along their height in this experiment is an interesting question. Also, why did the experimental plants not start with their leaf area at high positions from the start, thereby immediately shading types with leaves at lower positions? It might be that we overestimate the benefits of a change in crown shape, or underestimate the costs that are involved.

To answer these questions, we use a mechanistic model on plant growth. We provide the model plants with the ability to change crown shape on the basis of a shading signal, as well as the ability to grow plastically in height. We explicitly include costs for these processes. We investigate the effect of plasticity in crown shape as well as differences in the rate with which plants can change the shape of their crown, and how this interacts with their height growth.

Methods

Plant growth model

As a basis, we use the model that was already developed in Chapter 2. An elaborate explanation of the model is given in that chapter. While in the original model plants grew according to an allometric relation between plant height and plant volume, in this chapter plants grow according to a pipe model (Shinozaki et al., 1964a,b). The allometry between stem height and volume is determined by this pipe model theory. The leaves, the height and the position of leaves along the height of the plant will determine the required pipe (and thus stem-) volume. Figure 1 is a schematic representation of the relation between stem volume and the height of the leaf area.

Leaves have different costs for construction and maintenance, depending on the plant height and the position of the leaves along the height of the plant. This is because a certain amount of stem has to support these leaves, in accordance to pipe theory. It is assumed that plants have a cylinder-shaped crown. Within this cylinder, leaf area density can vary vertically. Horizontally, per layer, leaf elements are evenly distributed over the cross-section of the cylinder. All horizontal pipes therefore have the same average length. We assume this does not change with the height of the plant.

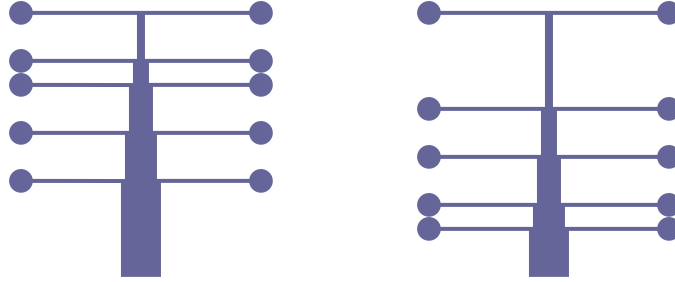


Figure 1. Example of how crown shape affects stem volume. In the left hand drawing, leaf area is positioned towards the top of the plant. In the right hand drawing, leaf area is positioned towards the lower parts of the plant. Consequently, the total stem volume for the plant is less in the right hand drawing.

To evaluate the performance of plants, we need a fitness measure. During growth, the plant stores a constant proportion of the net photosynthetic production. It is assumed that this stored carbon can be transformed into seed at the end of growth. The lifetime storage of carbon is thus a measure of fitness for the model plants. Below we will discuss the features of the extended model in more detail.

Crown shape of the plants

The plants in the model have an explicit crown shape, expressed in vertical leaf area density. At every height, the leaf area situated at that height is known. The leaf area distribution in leaf area per centimetre height is described by the following formula (Caton et al., 1999):

$$\text{Leaf area distribution} \quad \lambda(h)_t = p_0 \cdot \frac{L_t}{h_{pt}} \cdot \left(\frac{h}{h_{pt}} \right)^{p_1} \cdot \left(1 - \frac{h}{h_{pt}} \right)^{p_2} \quad (7.1)$$

In which h_{pt} is the height of the plant at time t , L_t is leaf area index at time t , h is the height at which the leaf density is calculated and p_0 , p_1 , p_2 are shape parameters. The shape of the crown is not necessarily rigid; it can change depending on the shape parameters p_1 and p_2 . The parameter p_0 is a normalisation parameter (see Formula 1.3 in Chapter 2). We can consider plant shapes in which the leaf area is mostly at the lower part of the stem, or at the topside. For examples of crown shapes, see Appendix 1 in Chapter 2.

The relation between shade and growth patterns

It can be argued that a plant that has its leaf area in a high position in the vegetation canopy, will receive more of the available light. Possibly, plants that experience shade, will try to bring more leaf area higher up in the vegetation canopy. This can be done either by changing the crown shape in a way that more of the leaf area is positioned at the topside of the plant or by increasing the plant's height. It is assumed therefore that the plant is able to increase height investment on the basis of a shade signal, and bring leaf area upwards on the basis of the same signal. The amount of shade that is experienced is taken as a measure for the plants to start improving their position in the vegetation canopy (Smith, 1982). For calculation of the shading signal S_{signal} , see Section 5 in Chapter 2. No distinction is made between shading by neighbours and self-shading.

The change in crown shape and costs

The extent and speed of either height growth or a change in crown shape can be varied. For the change in crown shape, we introduce a reaction norm r . With larger r , the intensity of a change in crown shape is higher.

$$\text{Shading signal} \quad \tau = S_{signal} \cdot r \quad (7.2)$$

Here S_{signal} is the shading signal and r the reaction norm of the plant for the shading signal. The change in shape occurs by means of a change in the shape parameters p_1 and p_2 . Suppose that the change in p_1 and p_2 as a result of the signal τ is related as follows:

$$\text{Change in shape parameters} \quad d_{\tau} p_2 = -d_{\tau} p_1 \quad (7.3)$$

If the plant is supposed to bring its leaf area higher along the stem, p_1 has to increase. From equation (7.3) it can be derived that for every increase of p_1 , p_2 decreases with the same amount. To prevent the parameters p_1 and p_2 from going below zero, the rate of change of p_1 is made dependent on some maximum value of the parameter p_1 . It has to be noted that the maximum value p_{1max} has to be taken such that, if it is reached, the parameter p_2 is still positive.

$$\text{Crown shape rate} \quad d_{\tau} p_1 = p_1 \cdot (p_{1max} - p_1) \cdot d_{\tau} \tau \quad (7.4)$$

Figure 2 shows the effect of the reaction norm r on the leaf area distribution of growing single, isolated plants at different time steps.

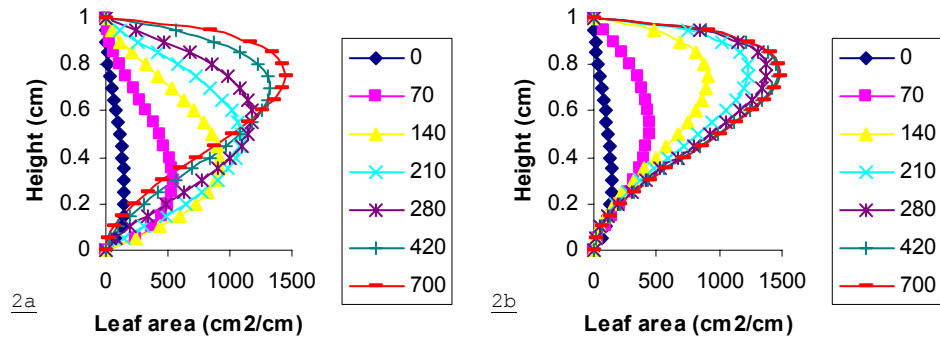


Figure 2. Effect of the reaction norm r on the leaf area distribution at different time steps during growth. Plants in these figures have no height growth. Start values $p_1 = 0.6$, $p_2 = 2$. Maximal p_1 $P_{1max} = 2$. Reaction norm $r = 0.02$ (a) and $r = 0.1$ (b).

Obviously, with a change in crown shape, leaf area has to be constructed or cast away at certain positions along the height of the plant. For the calculation of the rate of change in total leaf area with a change in shape parameters (as a result of the shading signal) see Appendix 2.

With a change in crown shape, costs for construction of leaf and pipe elements are involved. Per unit of leaf area that has to be newly constructed, a certain amount of pipes needs to be made for support. The higher the unit of leaf area is situated along the height of the plant, the longer the pipes need to be and the more the leaf area costs in terms of construction. See Appendix 3 for a calculation of costs. Per unit of leaf area that is discarded with a change in shape, carbon can be partly retracted from the leaves. The structural mass of the pipe that was used to support the leaf area is discarded and not taken into account in the carbon balance any longer. The change in crown shape is not related to the carbon available from net photosynthetic production. If costs exceed the available carbon, leaf area is cast away and retrievable carbon within these leaves is used to pay for the costs.

The height growth and costs

The investment in height growth increases with the severity of the shading signal. Height investment is thus plastic. The investment in height is always a proportion of net photosynthetic production. Because we want to investigate the interplay of height investment and a change in crown shape, we distinguish plants that invest different proportions of net photosynthetic production in height. Every plant has been assigned a maximum portion of net photosynthetic production that can be allocated to height growth (see Table 1). Depending on the severity of the shading signal, a fraction of this maximum

is allocated for the construction of pipes. The maximum investment in height is done if the plant is completely shaded. Table 1 shows the types that differ in maximal height growth investment.

Table 1. Types differing in maximum height investment (gram carbon per gram carbon obtained from net photosynthetic production (npp)). Height investment increases with the severity of the shading signal but can never exceed the maximum height investment.

	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6
Maximum height investment (fraction of npp)	0	0.2	0.4	0.6	0.8	1.0

In former chapters, we assumed an allometric relation between stem volume and height. With the introduction of pipes, the leaf area and its distribution over the height of the plant will determine the height increment. To maintain the crown shape, leaf has to be constructed at the top of the plant, while leaves are discarded at the base of the plant (see also Makela, 2002). If a lot of the leaf area is positioned at the top of the plant, a large pipe volume will be needed to replace this leaf area. The plant will be able to grow in height just a little on the carbon allocated to height growth. Contrastingly, plants with most of the leaf area at low positions along their height will have low pipe costs for the reallocation of leaves and will be able to achieve a proportionally faster height growth. The calculation of leaf area reallocation with height growth is described in Appendix 2 of Chapter 2. See Figure 4 in Chapter 4 for an example of leaf area reallocation with a difference in leaf area position.

Maintenance of structural biomass

With the introduction of pipes, the maintenance of leaf area does not scale linearly anymore with leaf mass. The vertical position of the leaf area determines the length of the supporting pipes. The higher the positioning of the leaf area, the higher the maintenance costs for a plant. The calculation of the maintenance costs is formalised in Appendix 5. In order to keep plant leaf area and height characteristics comparable to those of former chapters, the maintenance coefficient was set from 0.0235 to 0.0435 gram C per gram C structural mass. This maintenance coefficient is slightly outside the realistic range (0.01 to 0.03) for maintenance (Goudriaan & van Laar, 1994), implying that this model misses some process or characteristic that would increase the maintenance costs, or reduce income from net photosynthetic production. Varying the maintenance costs, however, did not affect the patterns as observed in this chapter, implying that they are robust patterns.

Results

For reasons of simplicity, all simulations are done within a fixed simulation period (700 time steps) and an unvarying light climate.

Single plant performance

The growth of plants is rather complicated because the height growth trades off with the leaf area production, while the leaf area determines the costs for height growth. A change in crown shape will incur costs as well. Figure 3 depicts the carbon storage for seed production, final height and leaf area with height growth for single, isolated plants with and without a change in crown shape.

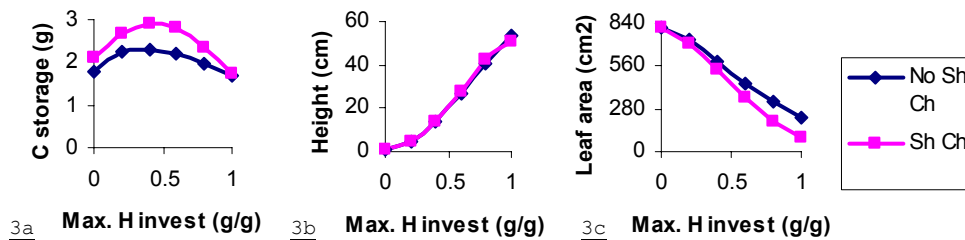


Figure 3. Performance of single, isolated plants differing in height investment. For an explanation on height investment types, see Table 1. Plants are able to change their crown shape (ShCh) or not (No ShCh). Depicted in this figure are: stored carbon (a), attained height (b), attained leaf area (c).

A plant type with average maximal height investment of 0.4 has the highest storage of carbon both with and without shape change. Interestingly, the plants with the ability to change shape have stored more carbon than types without shape change. As shape change incurs extra carbon costs for the reallocation of leaves (see Appendix 3) on top of the costs for height growth, there has to be an advantage of some sort with shape change. The explanation lies in the time to reach steady state. Steady state is the point where the costs of maintenance of biomass equal the income from gross photosynthetic production. At this point no growth occurs and carbon is not stored any longer. Plants that change their crown shape grow less rapidly in leaf area (in the low height growth types 0 to 0.4) or even decrease their leaf area near steady state (in the higher height growth types 0.6 to 1.0) (data not shown). For these plants, the time to reach steady state is longer and during this period more carbon can be stored.

Competing plants, no height growth

For competing plants, we assume that crowns completely overlap horizontally. Plants, however, can differ in height and the distribution of leaves over their height. It is logical to assume that, at equal plant height, a plant that already has or brings its leaf area more towards the top, intercepts more light than a plant that does not. Consequently, its ability to store carbon will be higher. We will start by checking this basic assumption. The plants in this simulation have no height growth, so the differences in performance originate from differences in their abilities to change crown shape. Plants start out with $p_1 = 0.6$ and $p_2 = 2$. This corresponds with the crown shape found on average in the experiment (see Table 5 in Appendix 1). Although the shade signal dictates the change of the crown shape, this effect can be enlarged or downgraded by introducing a reaction norm r (see Formula 7.2 and Figure 2). We also make a distinction in the extent of the change in shape, which is dictated by parameter p_{1max} (see Formula 7.4). The results are shown in Figure 4.

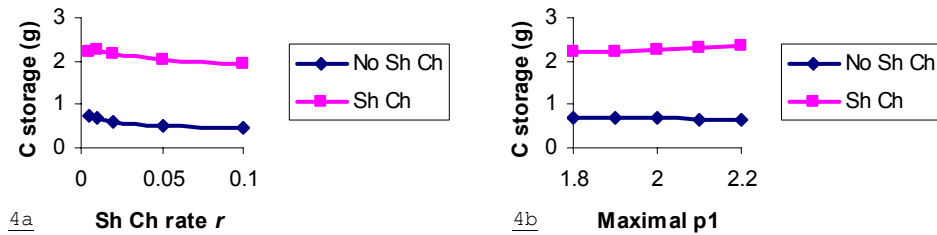


Figure 4. Storage of carbon for competing plants. Plants within a pair are able to change their crown shape (ShCh) or not (No ShCh). Plants with the ability to change their crown shape differ in the rate r with which they change their shape (a) or the extent p_{1max} to which they change their shape (b).

Figure 4 shows that, if no height growth is involved, an ability to change crown shape is indeed a competitive advantage. Plants that are able to change their crown shape consistently have higher carbon storage than plants that are not able to change their crown shape. The explanation of the pattern shown in Figure 4a is that a high rate of change in shape results in increased lifetime shading of the plant without a change in crown shape, and thus reduces its lifetime carbon storage. At the same time, a high rate of a change in shape is costly for the plant with the ability to change its crown shape. Lifetime maintenance costs are higher for this plant because leaves at a high position cost more than leaves at a lower position. With an increase in the rate at which the shape changes, lifetime carbon storage is thus slightly less.

Figure 4b shows that an increase in the p_{1max} increases the carbon storage of the plants with the ability to change crown shape. The leaf area increases at a lower pace.

This keeps the plant from growing in to steady state, allowing it to prolong the carbon investment in storage. Plants with higher p_{1max} slightly reduce performance of the plant that does not possess the ability to change crown shape. The increased shading of this subordinate plant causes this.

Competition between height investment types

In the simulations on plants that did not invest in height we saw that changing the crown shape was beneficial in a competitive situation. In the simulations on single isolated plants with height investment, in the previous section, carbon storage for seed was also higher for plants with the ability to change crown shape. However, a change in crown shape caused a smaller leaf area, which is an important feature in the competition for light. The final attained leaf area became smaller with increasing height investment.

In the rest of this chapter, reaction norm r is 0.01 and p_{1max} is 2. The initial shape for all plants is determined by the parameters $p_1 = 0.6$, $p_2 = 2$. In the following simulations we examine pairs of competing plants with different maximal height investment (see Table 1), either with or without the ability to change their crown shape. Table 2 depicts the carbon storage that is realised for pairs of types without the ability to change their crown shape. Table 3 shows the carbon storage when competing plants do have the ability to change their crown shape.

The results in Table 2 show that, for the types without the ability to change the shape of their crown, the type with 0.6 height investment wins from both higher and lower height investment types. The results in Table 3 show that for types with the ability to change crown shape type 0.4 wins from both higher and lower height investment types. A change in the shape of the crown apparently reduces the optimal height investment, in this case from 0.6 to 0.4 (see Table 2 and 3). A change in crown shape is thus unfavourable for types with a large height growth. This is caused by the large leaf area that has to be reallocated with increasing height growth when the leaves are higher along the stem of the plant. Additionally, maintenance of leaves at a high position costs more with increasing height.

CHAPTER 7

Table 2. Stored carbon for competing plants, differing in maximal height investment (max) (see Table 1), without the ability to change their crown shape. Within a cell, the carbon storage of the lower height investment type is in the left upper corner and of the higher height investment type it is in the right lower corner. The winning type in a combination is written in bold.

	Max 0.0	Max 0.2	Max 0.4	Max 0.6	Max 0.8	Max 1.0
Max 0.0	-	0.45	0.55	0.68	0.83	0.97
Max 0.2	-	2.03	1.88	1.68	1.45	1.18
Max 0.4	-	-	0.63	0.75	0.92	1.04
Max 0.6	-	-	1.82	1.61	1.34	1.04
Max 0.8	-	-	-	0.86	1.02	1.23
Max 1.0	-	-	-	1.52	1.07	0.72
Max 0.0	-	-	-	-	1.03	1.33
Max 0.2	-	-	-	-	0.71	0.52
Max 0.4	-	-	-	-	-	0.95
Max 0.6	-	-	-	-	-	0.56
Max 0.8	-	-	-	-	-	-
Max 1.0	-	-	-	-	-	-

Table 3. Stored carbon for competing plants, differing in maximal height investment (max) (see Table 1), with the ability to change their crown shape. Within a cell, the carbon storage of the lower height investment type is in the left upper corner and of the higher height investment type it is in the right lower corner. The winning type in a combination is written in bold.

	Max 0.0	Max 0.2	Max 0.4	Max 0.6	Max 0.8	Max 1.0
Max 0.0	-	0.45	0.56	1.70	1.90	1.84
Max 0.2	-	2.96	3.09	2.30	1.53	1.10
Max 0.4	-	-	0.64	1.78	2.15	2.30
Max 0.6	-	-	2.94	2.07	1.32	0.91
Max 0.8	-	-	-	1.80	2.24	2.45
Max 1.0	-	-	-	1.42	0.85	0.60
Max 0.0	-	-	-	-	1.50	1.63
Max 0.2	-	-	-	-	0.76	0.52
Max 0.4	-	-	-	-	-	0.95
Max 0.6	-	-	-	-	-	0.56
Max 0.8	-	-	-	-	-	-
Max 1.0	-	-	-	-	-	-

Competition between types with equal height investment

We have evaluated the effect of a change in crown shape on the fitness of different competing height investment types. When the plants had the ability to change their crown

shape, the optimal height investment was lower compared to plants that did not change their crown shape. Apparently, there is a trade-off between a change in crown shape and height growth. At which intensity of height growth is it beneficial to invest in a change in crown shape, and at which intensity does it become better to invest in height growth? We compare the fitness of pairs of types with equal height investment, but differing in their ability to change the shape of the crown, to answer this question (Figure 5).

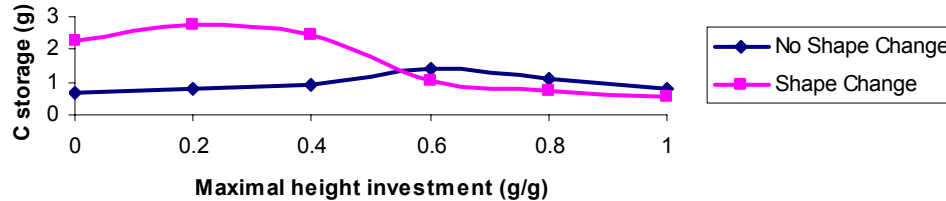


Figure 5. Storage of carbon for competing pairs of types with equal height investment but differing in ability to change their crown shape. For an explanation of different maximal height investment types, see table 1.

Figure 5 shows that the relative fitness advantage of a change in crown shape becomes a disadvantage at higher height investments. From these results we can conclude that it is beneficial for plants to have a low height investment and the ability to change shape, or to have a large height investment and not to change their crown shape. If the optimal type without the ability to change its shape (0.6 maximal height investment) (see Table 2) competes with the optimal type with the ability to change its shape (0.4 maximal height investment) (see Table 3), the type with the larger height investment wins (see Table 4).

Table 4. Performance of competing types. Type 0.4 with- and type 0.6 without the ability to change the shape of the crown. For an explanation of types, see table 1.

	Carbon Storage (g)	Height (cm)	Leaf area (cm ²)
Type 0.4, with change in crown shape	1.092	25.81	64.4
Type 0.6, no change in crown shape	1.342	51.65	302.2

It can be concluded from these simulations that height investment is a more important asset to determine competitive vigour than the ability to change the shape of the crown.

Rigid high- or low-positioned leaf area

In the experiment, described in the introduction and in Appendix 1, plants did not change their crown shape in any of the treatments. We saw in the model simulations that a change in crown shape was not beneficial for plants with a high investment in height. But what about plants that do not change the position of their leaf area from low to high, but already start with leaves in a high position? Figure 6 gives the carbon stored for seed production of plants with different height investments and leaves at a high or a low position along their height.

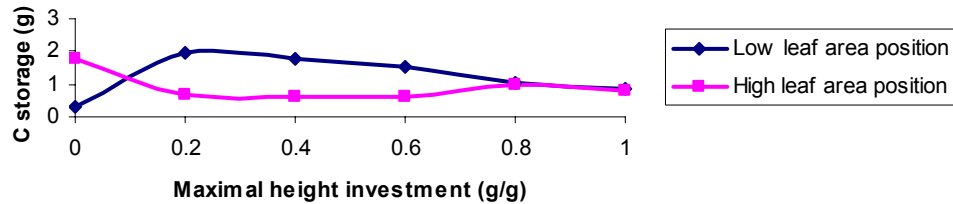


Figure 6. Carbon storage for competing pairs of types with equal height investment (Table 1) but differing in positioning of leaves along their height. For the plant with low leaf area $p_1=0.6$ and $p_2=2$. For the plant with high leaf area $p_1=2$ and $p_2=0.6$.

Figure 6 shows that a high positioning of leaves along the height is not beneficial in all simulations except the simulation where the plants do not grow in height. The explanation lies in the fact that plants with leaf area at high position along their height continuously have high costs for the reallocation of leaves with height growth and also high maintenance costs for these leaves. At very high maximal height investment, the performance of plants becomes similar. This is because the leaf area of all plants decreases substantially and therefore shading of the subordinate plant is less. The plant with leaf area at high positions has not reached steady state when the plant with the leaf area at low positions has. Therefore, the plant with its leaf area at a high position can continue to store carbon for a longer period of time than the plant with its leaf area at a low position.

Discussion

In contrast to prior expectations, plants in the competition experiment that was performed did not bring more of their leaf area to positions higher along the stem (i.e. change their crown shape) under more competitive circumstances. Plants did show an increase in height when competing within a canopy of tall plants, in comparison to competing within

a canopy of lower plants. With help of a dynamic model with elements of pipe model theory (Shinozaki et al., 1964a,b) we tried to gain insight in costs and benefits of a change in crown shape in relation with height growth.

Simulations with the model revealed that for single isolated plants, fitness was higher for plants with the ability to change crown shape. The resulting lower leaf area growth kept the plant away from steady state, allowing it to prolong growth. The benefits of a change in crown shape in competitive circumstances, however, were limited. A change in crown shape was beneficial in competition only when plants had low height investment. Moreover, an early (immediate) high position of leaves or very fast change in crown shape was not beneficial for plants of any height investment. Height growth was more effective in gaining a competitive advantage than a change in crown shape. In contrast, Yokozawa et al. (1996) investigated the effect of (rigid) vertical foliage profile on coexistence patterns of simulated tree species and found that a species with its leaf area positioned high along its stem could invade a stand of plants with leaf area at lower vertical positions, and also withstand invasion from such plants. In terms of stand stability or invasiveness, the plant with leaf area higher along the stem was the superior competitor. However, Yokozawa et al. (1996) did not include costs for leaf area reallocation with height growth.

One of the reasons that a change in crown shape is not beneficial in our study is the high cost associated with a change in crown shape, especially in combination with height growth. With more leaf area at high positions, a lot of leaf area is turned over with an increase in height. The maintenance of highly positioned leaf area is more costly as well. However, a plant that invests less in its leaf structure will have fewer costs replacing these leaves and would be able to afford a higher turnover of leaves. This may also play a role in plants that increase their specific leaf area (SLA), and thus increase their leaf area but decrease the carbon cost per unit of leaf area. Plants in a natural environment may also economize on defence against predators or other leaf traits that enhance longevity. All these measures would lessen costs per unit leaf area and increase possibilities for leaf turnover. The benefit of having low costs for the construction of leaf area is apparent in the many studies that find that species having fast growth and high turnover are able to increase the position of their leaf area (Werger & Hirose, 1988; Hikosaka et al., 2001).

Nutrient availability also affects the plant's investment in a change in crown shape. For example, in an experiment of Schippers (2000) several single, isolated grassland plants increased the height of their leaf area after 16 weeks of growth only at the highest nutrient level.

With increasing density it is also more beneficial to have leaves higher up in the vegetation canopy. An increase in height proved to benefit plants in increasingly dense vegetation stands (e.g. Givnish, 1982; Schwinning & Weiner, 1998; Chapter 4 this thesis). Few studies are available that investigate the benefits of relative leaf area position in increasingly dense plant stands. In their modelling study, Iwasa et al. (1984) found that both the optimal height and the position of the leaf area along the height increased with increasing plant density. This optimal plant shape was calculated however in an instantaneous static environment and the time course of costs and benefits was not

included. Nevertheless, experimental studies confirm that in dense stands, leaves are on average placed higher up along the stem than in open stands (Werger & Hirose, 1988; Weiner et al., 1990; Hikosaka et al., 2001). Additional simulations with the model in this chapter confirmed this phenomenon as well (data are not shown).

To conclude, we saw in our model simulations that a change in crown shape is beneficial in principle for single, isolated plants but not for plants in a competitive setting that also invest strongly in height growth. Possibly, a change in crown shape in a vegetation canopy is beneficial for plants that have already gained a dominant position in the vegetation canopy. These plants might experience less competitive pressure (Sterck & Bongers, 2001) and behave like 'single plants'. It is frequently observed that dominant individuals gradually develop an umbrella shaped crown (Morales et al., 1996; Shmida et al., 2000), which indicates that most leaf area at that time is situated at the top of their height. In a study of Ojea et al. (1988), *Ulex europaeus*, a fast growing shrub, showed the increase of average height of green foliage was higher as plants were taller. Puentes & Basanta (2002) found the same phenomenon. Makela & Vanninen (1998) found that Scots Pine trees responded in two ways to increase in stand age. Firstly, the crown base was lifted, by allocating new foliage higher up. Secondly, sparser crowns were grown. We hypothesise that a change in crown shape is not beneficial during competition because it interferes with height growth, which is of more importance for competitive vigour. More towards the end of stand development, when competitive pressure is less for surviving individuals, a change in crown shape will be more beneficial because the changing crown shape keeps the plant away from steady state, allowing it to have prolonged growth.

Appendix 1. The experiment

Seeds were collected in 1992 in the Gerendal, a chalk grassland in South Limburg, The Netherlands. Seeds were sown at 8 November 1995 in a 1:1 mixture of riversand:earth. After four weeks the plants were transplanted in a 5:1 mixture of riversand:marl in plastic containers of 21 cm diameter (5 litre). Plants were grown at a density of 10 plants. For the mixed culture, a target plant was planted in the middle of the container, surrounded by 9 plants of the other species. In the monoculture, plants were planted in the same pattern. The containers were fertilized weekly, at two different nitrogen levels. The high level was equivalent to 200 kg / ha/ yr and the low level was equivalent to 20 kg / ha/ yr. Three harvests were done, each three weeks apart. The first harvest was done four weeks after the transplantation of the seedlings in the plastic containers. Per harvest, five replicas were chosen randomly. Only the plant in the middle was used for analysis. The above ground part was harvested in layers of 5 cm in height from 0 to 15 cm, and in layers of 10 cm from 15 to 45 cm. At each harvest, the leaf area in the different layers was measured using a leaf area meter (Licor 3100, Lambda instruments Corp., Lincoln, Nebraska, USA).

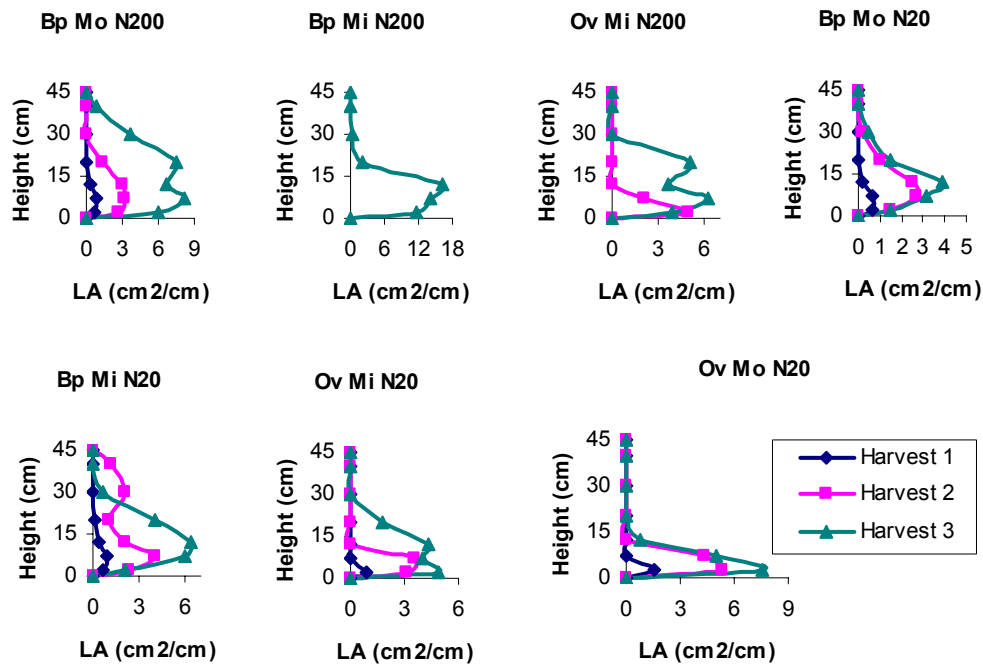


Figure 7. Leaf area distributions (LA, cm² per cm height) of the experimental plants *Brachypodium pinnatum* (Bp) and *Origanum vulgare* (Ov) (n=5) at three points in time (Harvest 1,2,3). Individual plants were grown with con specifics (Mo) or hetero specifics (Me) at different Nitrogen levels; 20 kg/ha/yr (N20) and 200 kg/ha/year (N200).

Some treatments were not measured because too little replicas remained. Of the remaining treatments, the leaf area per unit of height (average of five replicates) in the different layers was calculated (see Figure 7).

Experimentally obtained crown shapes were fitted with the crown shape function (see formula 7.1). We fitted only those plants that had more than three leaf area measure points (e.g. plants that were larger than ten centimetres). A very good fit could be achieved between measured and formula crown shape (see correlations in Table 5).

Table 5. Fitted shape parameters p_1 and p_2 (see Formula 7.1) to experimental crown shapes, correlation coefficient between fitted and measured crown shapes and average leaf area height (see 'bulk height' in Appendix 1 in Chapter 2) of different treatments and harvests. Parameters were adjusted until the fit did no longer improve. For an explanation on the used codes, see Figure 7. Only treatments with sufficient replicas and a total plant height larger than 10 cm were analysed.

		Bp Mo	Bp Me	Ov Me	Bp Mo	Bp Me	Ov Mo	Ov Me
		N200	N200	N200	N20	N20	N20	N20
Harvest 1	P1	0.6			0.6	0.6		
	P2	2			2.3	2		
	LA Height	0.23			0.21	0.23		
	Correlation	0.996			0.995	0.985		
Harvest 2	P1	0.3		0.6	0.6	0.1		
	P2	1.2		2	2.5	0.6		
	LA Height	0.2		0.23	0.19	0.14		
	Correlation	0.994		0.998	0.982	0.832		
Harvest 3	P1	0.6	1.3	0.3	0.9	1.3	0.8	0.7
	P2	2	5.5	0.6	2.9	3.5	2.4	2.5
	LA Height	0.23	0.19	0.33	0.24	0.27	0.17	0.22
	Correlation	0.975	0.957	0.957	0.973	0.999	0.962	0.999

Appendix 2. Leaf area redistribution with crown shape change

The change in crown shape occurs on the basis of the signal τ (see formula 7.2). The plant changes in shape by adjusting the parameter p_1 and p_2 . The change in leaf area with signal τ can be formulated as:

$$d_t \lambda = \left[\partial_{p_1} \lambda \cdot d_\tau p_1 + \partial_{p_2} \lambda \cdot d_\tau p_2 \right] \cdot d_t \tau \tag{2.2}$$

The derivatives $\partial_{p_1} \lambda$ and $\partial_{p_2} \lambda$

To find the rate of a change in leaf area over the height of a plant with a change in parameter p_1 and p_2 , we differentiate with respect to p_1 (the derivation for p_2 will be found in a completely analogous way). The change of leaf area with p_1 can be written as:

$$\partial_{p_1} \lambda = \frac{L}{h_p} \cdot d_{p_1} \left[p_0(p_1, p_2) \cdot \left(\frac{h}{h_p} \right)^{p_1} \cdot \left(1 - \frac{h}{h_p} \right)^{p_2} \right] \quad (2.3)$$

Which can be rewritten as:

$$\partial_{p_1} \lambda = \frac{L}{h_p} \cdot \left[\partial_{p_1} p_0 \cdot \left(\frac{h}{h_p} \right)^{p_1} \cdot \left(1 - \frac{h}{h_p} \right)^{p_2} \right] + \frac{L_t}{h_p} \cdot \left[p_0 \cdot \partial_{p_1} \cdot \left(\frac{h}{h_p} \right)^{p_1} \cdot \left(1 - \frac{h}{h_p} \right)^{p_2} \right]$$

The term $\left(\frac{h}{h_p} \right)$ is taken as x . The term $\left(\frac{h}{h_p} \right)^{p_1} \cdot \left(1 - \frac{h}{h_p} \right)^{p_2}$ is called $f(x)$. We make

use of the rule $d_x a^x = \ln(a) \cdot a^x$. Now the formula can be written as:

$$\partial_{p_1} \lambda = \frac{L}{h_p} \cdot \left[\partial_{p_1} p_0 \cdot f(x) \right] + \frac{L}{h_p} \cdot \left[p_0 \cdot \ln \left(\frac{h}{h_p} \right) \cdot f(x) \right] \quad (2.5)$$

To find the derivative $\partial_{p_1} p_0$ we use the expression for p_0 , which is specified as

$$p_0 = \frac{1}{\int_0^1 d_x (x)^{p_1} \cdot (1-x)^{p_2}} = \frac{1}{F(x, p_1, p_2)} \quad (2.6)$$

Hence, making use of the quotient-rule to obtain the right hand term, we obtain

$$\partial_{p_1} p_0 = d_{p_1} \left[\frac{1}{F} \right] = \frac{-1}{F^2} d_{p_1} F \quad (2.7)$$

The change of F with a change in p_1 is

$$\partial_{p_1} F = d_{p_1} \left[\int_0^1 d_x (x)^{p_1} \cdot (1-x)^{p_2} \right] = \int_0^1 d_x d_{p_1} \left[(x)^{p_1} \cdot (1-x)^{p_2} \right] \quad (2.8)$$

And so

$$\partial_{p_1} F = \int_0^1 d_x \ln(x) \cdot (x)^{p_1} \cdot (1-x)^{p_2} \quad (2.9)$$

Now we can write the full equation for $\partial_{p_1} p_0$

$$\partial_{p_1} p_0 = \frac{-1}{\left[\int_0^1 d_x (x)^{p_1} \cdot (1-x)^{p_2} \right]^2 \cdot \int_0^1 d_x \ln(x) \cdot (x)^{p_1} \cdot (1-x)^{p_2}} \quad (2.10)$$

To recall, the total equation for $\partial_{p_1} \lambda$ was, taking $(x)^{p_1} \cdot (1-x)^{p_2}$ as $f(x)$:

$$\partial_{p_1} \lambda = \partial_{p_1} p_0 \cdot f(x) + p_0 \cdot \partial_{p_1} f(x) \quad (2.11)$$

Now, the whole equation for $\partial_{p_1} \lambda$ is, taking $\int_0^1 d_x (x)^{p_1} \cdot (1-x)^{p_2}$ as $F(x)$:

$$\partial_{p_1} \lambda = - \left[\frac{1}{F^2} \cdot \int_0^1 d_x \ln(x) \cdot f(x) \right] \cdot f(x) + p_0 \cdot \ln(x) \cdot f(x) \quad (2.12)$$

This can be simplified to (using $p_0 = \frac{1}{F}$):

$$\partial_{p_1} \lambda = f(x) \cdot \left[-p_0^2 \cdot \int_0^1 d_x \ln(x) \cdot f(x) + p_0 \cdot \ln(x) \right] \quad (2.13)$$

Now, the partial derivative for p_1 in this formula is

$$\partial_{p_1} \lambda = p_0 \cdot f(x) \cdot \left[\ln(x) - p_0 \cdot \int_0^1 d_x \ln(x) \cdot f(x) \right] \quad (2.14)$$

And, completely analogous, the change in λ with a change in the parameter p_2 :

$$\partial_{p_2} \lambda = p_0 \cdot f(x) \cdot \left[\ln(1-x) - p_0 \cdot \int_0^1 d_x \ln(1-x) \cdot f(x) \right] \quad (2.15)$$

The derivative $d_t \lambda$

Since we assume that $d_\tau p_2 = -d_\tau p_1$ (see formula 7.3) the change in leaf area over time with a change of the signal τ can be written as

$$d_t \lambda = \left[\partial_{p_1} \lambda \cdot d_\tau p_1 + \partial_{p_2} \lambda \cdot (-d_\tau p_1) \right] \cdot d_t \tau = \left[\partial_{p_1} \lambda - \partial_{p_2} \lambda \right] \cdot d_\tau p_1 \cdot d_t \tau \quad (2.17)$$

Using the expressions for $\partial_{p_1} \lambda$ and $\partial_{p_2} \lambda$ this gives:

$$d_t \lambda = \frac{L}{h_p} \cdot p_0 \cdot f(x) \cdot \left[\ln(x) - p_0 \cdot \int_0^1 d_x \ln(x) \cdot f(x) \right] - \frac{L}{h_p} \cdot p_0 \cdot f(x) \cdot \left[\ln(1-x) - p_0 \cdot \int_0^1 d_x \ln(1-x) \cdot f(x) \right] \cdot d_\tau p_1 \cdot d_t \tau \quad (2.18)$$

The terms $\frac{L}{h_p}$, p_0 , and $f(x)$ can be taken outside brackets. Since integrals over the same

interval can be combined, and using the rule $\log(a) - \log(b) = \log\left(\frac{a}{b}\right)$ we obtain:

$$d_t \lambda = \frac{L}{h_p} \cdot p_0 \cdot f(x) \cdot \left[\ln\left(\frac{x}{x-1}\right) + p_0 \cdot \int_0^1 d_x f(x) \cdot \ln\left(\frac{1-x}{x}\right) \right] \cdot d_\tau p_1 \cdot d_t \tau \quad (2.19)$$

Using the rule $\ln\left(\frac{1-x}{x}\right) = -\ln\left(\frac{x}{x-1}\right)$ we obtain

$$d_t \lambda = \frac{L}{h_p} \cdot p_0 \cdot f(x) \cdot \left[\ln\left(\frac{x}{x-1}\right) - p_0 \cdot \int_0^1 d_x f(x) \cdot \ln\left(\frac{x}{1-x}\right) \right] \cdot d_\tau p_1 \cdot d_t \tau \quad (2.20)$$

Appendix 3. Costs with a change in crown shape

When the plant changes its crown shape, leaf area has to be newly constructed at some positions along the height of the plant, whereas at other positions leaf area is cast away. There is a point h^* , where the rate of leaf area production is zero with a change in shape. If the plant changes shape so that relatively more leaf area gets positioned at higher

positions along the stem, leaf area is constructed above this point h^* . Below this point, leaf area is cast away. The point h^* is calculated as follows:

$$d_t \lambda = \frac{L}{h_p} \cdot p_0 \cdot f(x) \cdot \left[\ln\left(\frac{x}{x-1}\right) - p_0 \cdot \int_0^1 d_x f(x) \cdot \ln\left(\frac{x}{1-x}\right) \right] = 0 \quad (3.1)$$

So, the right hand part of the formula has to comply to

$$\ln\left(\frac{x}{x-1}\right) = p_0 \cdot \int_0^1 d_x f(x) \cdot \ln\left(\frac{x}{1-x}\right) \quad (3.2)$$

We make use of the rule: if $a = \ln(b)$ then $b = e^a$. This gives

$$\frac{x}{1-x} = \exp\left(p_0 \cdot \int_0^1 d_x f(x) \cdot \ln\left(\frac{x}{1-x}\right)\right) \quad (3.3)$$

Because $x = \frac{h}{h_p}$; h^* is:

$$h^* = \left(1 + \left(\exp\left(p_0 \cdot \int_0^{\frac{h_p}{h_p}} \left(\frac{h}{h_p}\right)^{p_1} \cdot \left(1 - \frac{h}{h_p}\right)^{p_2} \cdot \ln\left(\frac{\frac{h}{h_p}}{1 - \frac{h}{h_p}}\right)\right)\right)^{-1} \right)^{-1} \cdot h_p \quad (3.4)$$

The pipe costs can be divided in a vertical and a horizontal part. For any change in crown shape $d_t \lambda$, the costs for pipe construction can be calculated as the sum of the extra length of horizontal and vertical pipes.

$$\text{Cost for pipes} \quad C_p d_t L = \left[\int_{h^*}^{h_p} dh \cdot d_t \lambda \cdot c_p \cdot \frac{2 \cdot r_c}{3} + \int_{h^*}^{h_p} dh \cdot d_t \lambda \cdot h \cdot c_p \right] \quad (3.5)$$

Here c_p is the pipe volume per cm^2 leaf area per unit length, r_c is the radius of the crown, $\frac{2 \cdot r_c}{3}$ is the average length of the horizontal pipes of the plant.

Appendix 4. Costs for maintenance

The maintenance for the pipes associated with the leaf area is calculated as:

$$\text{Maintenance for pipes} \quad M_p = c_p \cdot \frac{2 \cdot r_p}{3} \cdot L + \int_0^{h_p} dh \cdot \lambda(h) \cdot h \cdot c_p \quad (4.1)$$

SUMMARY AND GENERAL DISCUSSION

Aims and method

It has long been recognised that competition is potentially an important determinant of the structure and composition of plant communities (Grace and Tilman, 1990; Goldberg & Barton, 1992). The mechanisms of competition are nevertheless poorly understood (Schwinning & Weiner, 1998; Berntson & Wayne, 2000). In search for explicit mechanisms behind the competition for light, and their influence on the coexistence of plants, we used a modelling approach. We investigated whether different investments in plant traits could cause patterns on community scale. Detailed growth patterns were incorporated in the plant growth model. The model that we constructed had three important properties. Firstly, growth was strictly on the basis of a carbon balance. No more carbon could be spent than was gained in photosynthesis. Secondly, the allocation to various parts of the plant and processes such as maintenance were specifically included. In many models, allocation trade-offs are implicitly assumed but rarely explicitly incorporated (de Jong & van Noordwijk, 1992). That it is important to determine the exact pattern behind a trade-off was shown in Chapter 4. Plants that differed in their timing of height investment also differed in competitive strength even though the total investment was the same. Also, in Chapter 6, plant types possessing a trade-off between seed production and vegetative growth behaved differently depending on the pattern of carbon investment. Possibilities for coexistence depended on whether the trade-off originated from the timing of a sudden switch to reproduction or the quantity invested in reproduction during a lifetime. Thirdly, plant architecture was incorporated. This determined the light interception of plants when growing alone or with other plants. We made a model with plants that contained only a few traits and then allowed one trait at a time to vary in value. This provided a good way to isolate the role of particular traits and assess the adaptiveness of different values of the trait. We investigated the role of investment in height growth, crown shape, investment in seed and dispersal distance of seed on the performance and coexistence of plants.

Coexistence under light competition

In the different simulations reported in this thesis, several factors promoting coexistence under light limitation were found. Interestingly, the role of any plant trait in itself for generating coexistence was limited. These plant traits, however, were the basis for less tangible factors that did affect coexistence. It was the interplay of plant traits with frequency and density dependent processes and the inclusion of space that generated possibilities for plants to live together. By the different susceptibility of plants with different traits to frequency, density and space, situations were created where each of the

types could be successful. We note explicitly here that the investment patterns of plants and the emerging traits were the actual mechanism through which all other processes worked.

In **Chapter 3** we found that if competing plants differ in height investment, the plant that invests more in height is always disadvantaged at higher frequency. Because it has to meet higher costs for stem production and maintenance, it needs higher light availability. If the frequency of plants with a high investment in height increases, the light interception per plant diminishes. The plants have less net photosynthetic production to invest in leaf area and growth is hampered. The performance of these plants diminishes. Consequently, plants with lower investment in height are less shaded and perform better than the plants with higher investment in height. This negative frequency dependent phenomenon caused plants of contrasting height investment to stably coexist. Not all pairs of types could coexist on the basis of this frequency dependence. Plants that invested approximately evenly in height growth and leaf growth (i.e. balanced growth) did not show negative frequency dependency. Both slightly lower and higher height investment types were out competed at any frequency. Only pairs with contrasting height growth (one with lower and one with higher than the type with balanced growth) could coexist.

When all types were included in the simulations simultaneously, in **Chapter 4**, no coexistence could occur. The type with balanced investment in height and leaf area growth excluded all other types. Nevertheless, when explicit space was incorporated, coexistence did occur. In this spatial environment, local density was variable as a result of the random distribution of individual plants. At increasing density, a plant type possessing a higher investment in height performed better than all other types. Within the different densities per locality that resulted from the random distribution of individuals, different height investment types found optimal conditions for growth. Up to four types could coexist stably in this kind of environment, and even more if the height investments of the types were taken closer together. We conclude that, for types that differ in their investment in height, random variation in density provides a means to coexist.

In the subsequent simulations in **Chapter 5**, we set the height investment constant for all types. Instead of constantly storing a portion of net photosynthetic production for the production of seed, the types now differed in their timing of a switch to an investment in seed production. As a result, types differed in their length of vegetative growth and thus in competitive vigour. There was a succession from low competitive types (but with high seed production) towards highly competitive types (but with low seed production). When reintroduction of extinct types was allowed, this succession repeated itself indefinitely. We can conclude that a simple trade-off between seed investment and vegetative growth can be cause for coexistence of types, although types in this case continually vary in frequency. In other words, this was coexistence under non-equilibrium circumstances.

When we introduced explicit space, in **Chapter 6**, we saw that several types differing in the timing or extent of seed investment could coexist. Although the types with extended vegetative growth were competitively superior, the types with a shorter period of vegetative growth were able to achieve a higher density at equilibrium. Coexistence took

place by means of a colonisation/competition trade-off. Although usually in models this result is obtained as a consequence of disturbances (and thus under non-equilibrium circumstances) we showed that the most competitive plant types in the system evolved towards types that were naturally limited in seed set and thus left enough space for other species to coexist. Plant types with lower competitive ability were not limited in seed set and left no empty space for other plant types. The performance of these types was however reduced in the presence of the most competitive type, to such an extent that several types differing in fecundity and competitive ability could coexist on the basis of this colonisation/competition trade-off. A large dispersal distance was beneficial for the less competitive types that survived by colonising empty spots.

In **Chapter 7**, we did not search for patterns of coexistence but rather evaluated the benefits and costs of a change in the shape of the plant's crown. It was found that plants could enhance their performance by casting away leaves, especially towards the end of growth. This kept the plant away from steady state and thus prolonged its growth. This however was only beneficial for single, isolated plants and not for plants under severe competitive pressure.

Possible influence of omitted traits

By omitting traits that plants obviously do possess in a real situation, the plant behaviour as found in this thesis does not give the whole picture. When other traits are introduced, the results obtained in this thesis will have to be reassessed. We have to bear in mind that results could be less relevant because certain restrictions or processes are overlooked. This does not make the simulations in this thesis less useful. With the simulations done, we can ponder on how results would differ if certain traits or processes are included. This in itself is a great step forward. With a more complex model, containing many traits, such insights could not have been gained. We will now discuss the possible influence of some additional traits. We focus on the influence of these additional traits on the possibilities for coexistence between different types.

Diameter growth

In the current model, plants grow in a predefined area of 10 by 10 centimetres. Types therefore do not differ in the ground surface they cover. Additionally, plants in the current model are rigid in the ground surface that they cover when growing from seedling to mature plant. Allowing differences in the investment in diameter growth will increase the strategy space for plants. Species that cover a larger area will have an increased potential for light interception while additionally experiencing a decrease in self-shading. Also, plants with a large investment in diameter growth can possibly largely avoid shade from plants that invest more in height growth and less in diameter growth. This would reduce competition and enhance the probability of coexistence. Another unrealistic assumption in the current model is that plants within the predefined area completely overlap with their leaf areas horizontally. This restriction can be relaxed by assigning specific coordinates

per plant. The overlap (a measure of influence) with other plants can consequently be defined on the basis of diameter and distance from other plants. On average the competitive pressure will decrease for there will be only a partial overlap. Competitive exclusion will be slower. Additionally, there will be more variation in competitive pressure within the vegetation. Especially small plants (in terms of diameter) will have a better chance of finding an empty spot (Dushoff et al., 2002). This would increase possibilities for coexistence.

Self-thinning

In the model, plants of all types are equal of shape at the start of growth. There is no variability in the timing of starting growth. All individuals within a type within a patch are equal from beginning to end of the simulation. Therefore, within plants of a type sharing a patch, there is no self-thinning. Self-thinning of plant populations is an inherent process to population development (Yoda et al., 1963; Kikuzawa, 1999). The origins of self-thinning are slight differences between individuals in a population. There can be, for instance, stochastic differences in growth caused by a difference in germination timing (Weiner & Thomas, 1986), or tissue damage by herbivory or trampling, or genetic differences in the expression of traits. If we would include some mechanism like this, self-thinning would occur in our model. We would avoid the situation where plants of similar types would have to divide the resource equally amongst them and therefore be all limited in size. Another way to create differences in growth would be –as discussed earlier- to provide plants with a unique set of coordinates. Differences in crown overlap will cause differences in growth rate and by asymmetric competition size differences will emerge. In the discussion of Chapter 5 we discuss plants that had a threshold biomass for reproduction. At high densities, none of the plants reached that threshold. Self-thinning would enable some individuals to reach the threshold size. Also, because only a few (and not all) would persevere to reproduce, large fluctuations in population size as a result of overproduction as we saw in Chapter 6 would less readily occur.

Root system and nutrients

Including a functional root system would only be useful if the acquiring of nutrients and water in the soil, and using them for growth processes, would be included specifically. This would pose the plant with the decision to either invest in aboveground matter to capture light, or invest in belowground matter to capture nutrients and water. The decision would depend on how limiting light, nutrients and water are for the growth of the plant. A plant will invest in the organ that is able to capture the resource that is most limiting for growth (Brouwer, 1983). In contrast to light availability, a nutrient flow is not unidirectional. Within the range of influence of their root system, plants can deplete the resource to an overall low level. No gradient is thus formed. In this respect the competition for light will differ from the competition for nutrients. In the current model, the root and shoot biomass were positively linearly related. Plants of all types had a constant root/shoot ratio. Because the competition for nutrients and use of nutrients by the plant differs from that of light, the optimal root/shoot ratio might differ among types and

also during growth. It can be expected that the incorporation of nutrients will influence the growth strategies as treated in this thesis. A larger leaf area for instance will be beneficial for light interception only in combination with corresponding larger nitrogen content. This will increase the need for a larger root system, which will in turn proportionally restrict the leaf area growth.

Perenniality

When considering plants with a perennial lifestyle, plants have the opportunity to invest either in survival into the next season or invest all in reproduction. Plants that have a starting biomass from the beginning of a season will have an advantage over plants that have to start as a seedling. Even though the population growth will be reduced due to investments in survival into the next year, eventually perennials can be expected to exclude annual plants in an area. Nevertheless, in the case of a disturbance, perennials have a chance of dying without having exploited their potential reproduction over a lifetime. It will depend on the frequency and extent of disturbances whether annual and perennial plants can coexist.

Other factors promoting coexistence

In this thesis we studied plants in a homogeneous environment. The single variable factor was light availability. All differences in the light environment were induced by the composition of the vegetation itself and not imposed by some external factor. Under these restricted circumstances we found several mechanisms that could allow for coexistence. In the real world, some heterogeneity e.g. in soil factors like nutrients or water, will be present. This enables plants to evolve some kind of niche differentiation. Niche differentiation theory has been a classic theory to explain species diversity (Diamond, 1975). Possibly, within each niche, factors as described in this thesis could still increase diversity.

Finally, we make a note on the timescales on which community composition should be studied. A co-occurrence of species at a single point in time is usually not considered as proof that these species can truly coexist. True coexistence, in most studies, is defined as a more or less permanent co occurrence of species (Chesson, 2000). To coexist, species should not go extinct at any point in the future. In other words, only species at permanent equilibrium coexist. However, it is unrealistic to assume that the lifetime of any species population will be indefinite. If a species can coexist on a time span longer than is relevant for a population or a community, this is equally relevant as permanent coexistence at equilibrium. So, if the outcome of a study is that the extinction of a species will occur eventually, but will take more than an ecological time-scale, it might as well be considered as permanent coexistence (Aarssen, 1992).

Away from equilibrium, possibilities for coexistence of different species might be larger. Various authors have noted that in the absence of disturbance, vegetations tend to evolve towards climax vegetation with only a few dominant species. In real

communities, those communities that have not yet reached equilibrium will tend to have higher species numbers than those that are at equilibrium (Whittaker, 1975; Guo, 2003).

As already mentioned, many studies search for stable coexistence. However, more recently the non-equilibrium view has begun to establish as an alternative (Caswell, 1982; Bauer et al., 2002). It is possible that some mechanism that promotes coexistence at non-equilibrium will prove to be the most important for the maintenance of diversity (Hutchinson, 1961). For grasslands, disturbance in the form of annual mowing, grazing or regular burning is common practice. Annual mowing and grazing affect the largest species most, thereby giving room for less competitive species (Bobbink & Willems, 1993). But even without disturbance species could persevere at non-equilibrium circumstances. Non-linear responses can give rise to oscillations or chaos (Hutchinson, 1961; Huisman & Weissing, 1999; Bauer et al., 2002). Within these oscillations or chaos, there will be differences in circumstances for growth. If these differences are reoccurring, species with different requirements for growth could find a regular window of opportunity. Species that were not viable at early stages of community development or species that were excluded in the course of community development could at some point in time (re-) enter the community. A criterion is that species are able to re-invade if numbers have got very low. In Chapter 5 we show that plant species can induce their own temporal variability, thereby allowing for numerous species to coexist in a cyclic manner.

The verification of model results

The results obtained in this thesis are a result of model simulations. Although model results can give clues to what the mechanisms behind plant growth and competition are, only the confirmation or rejection of these clues in an experimental setting will be conclusive. Because the assumptions in this model are explicitly formalised, they can be tested and falsified. If necessary, assumptions in the model that are less appropriate can be adjusted. Natural communities are unlikely to be appropriate systems to test the relatively simple assumptions made in the model. Phenotypic or genetic manipulations, or the comparison of closely related plant types that differ slightly in the expression of their traits, will give better systems to test the model predictions.

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SAMENVATTING IN HET NEDERLANDS

Dit proefschrift gaat over de vraag hoe planten zich met behulp van hun eigenschappen in een vegetatie kunnen handhaven. Door het hele proefschrift heen wordt van een simpel homogeen milieu uitgegaan, waarin planten om licht moeten concurreren. De planten in de vegetaties van dit proefschrift modificeren zelf de hoeveelheid licht die beschikbaar is. Zoals in een echte vegetatie ook het geval is, wordt licht door de verschillende lagen blad onderschept, waardoor er een verticaal licht gradient ontstaat. Hoe goed een plant presteert hangt van de verticale lichtgradient en de positie van het bladoppervlak van de plant in die gradient af. Dit bepaalt namelijk hoeveel licht een plant kan invangen en tegelijkertijd ook hoeveel licht er voor naburige planten overblijft. De hoogte van de plant en zijn (verdeling van-) bladoppervlak bepalen daarom in hoge mate de interacties tussen planten die om licht concurreren. De eigenschappen, die gerelateerd zijn met de hoogte en het bladoppervlak van een plant, zijn het gevolg van de allocatiepatronen voor deze plant eigenschappen. Vandaar dat in dit proefschrift van de allocatie patronen van planten wordt uitgegaan, in plaats van de eigenschappen op zich.

Onder de invloed van concurrentie kunnen planten (gedwongen of niet) hun allocatiepatroon veranderen. Concurrentie verandert dus de eigenschappen van hoogte en bladoppervlak en dit beïnvloedt weer de concurrentie tussen de planten. Planten, met hun beperkte levensduur, kunnen niet volstaan met ervoor te zorgen dat ze simpelweg niet weggeconcurrerd worden. Tijdens hun levensduur moeten er investeringen in nakomelingen worden gedaan om ervoor zorgen dat de eigenschappen van de plant ook in de volgende generatie blijven bestaan. Omdat investeringen in de ene eigenschap ten koste gaat van investeringen in andere eigenschappen, moeten planten een combinatie van eigenschappen vinden, die waarborgt dat ze door de jaren heen in een vegetatie gevestigd blijven. Met zoveel interacterende eigenschappen, die ook nog interacteren met de omgeving, is het moeilijk om de invloed van een bepaalde eigenschap op het succes van de plant te bepalen. Hierbij kunnen we gebruik maken van mechanistische modellen. Met behulp van een model kan de invloed van een eigenschap onderzocht worden zonder de interferentie van andere eigenschappen.

Met het model dat in dit proefschrift werd ontwikkeld, werden in de verschillende simulaties verscheidene factoren gevonden die voor coexistentie zorgden. Opvallend genoeg waren de eigenschappen zelf niet de directe oorzaak van coexistentie. Het samenspel van eigenschappen met frequentie, dichtheid en ruimte zorgde ervoor dat planten konden samenleven. Omdat planten met verschillende eigenschappen verschillend op omstandigheden met betrekking tot frequentie, dichtheid en ruimte reageren, waren er voor verschillende planten omstandigheden waarin ze succesvol konden groeien en reproduceren.

In **hoofdstuk 3** vonden we dat concurrerende planten, die verschillend investeren in hoogtegroeï, konden samenleven. De planten met een grote investering in hoogtegroeï werden in hun groei geremd als hun frequentie toenam. Dit werd door een verminderde lichtinvang, en de tegelijkertijd hoge kosten voor het maken en onderhouden van de

stengel veroorzaakt. Door de verminderde groei van de planten met een hogere investering in hoogtegroei konden de planten met een lagere investering in hoogtegroei juist beter groeien. Zij werden minder hevig overschaduwd. Dankzij deze negatieve frequentie-afhankelijke groei konden populaties van planten met grote en geringe hoogte-investeringen samenleven, zonder dat er een van de twee populaties uitstierf. Niet alle paren van planten met verschillende hoogtegroei konden overigens samenleven. Planten die ongeveer evenveel in blad als in stengel investeerden (planten met ‘gebalanceerde groei’) werden niet door veranderingen in frequentie beïnvloed. Planten die meer of minder investeerden dan dit type presteerden in concurrentie met dit type bij wat voor frequentie dan ook slecht. Alleen paren van planten met contrasterende investering in hoogtegroei (dus de een hoger en de ander lager dan de gebalanceerde investering) konden samenleven.

Wanneer we alle mogelijke typen van hoogte-investeerders met elkaar lieten concurreren, in **hoofdstuk 4**, bestond er geen mogelijkheid tot samenleven tussen de verschillende typen. Het type met gebalanceerde groei won van alle andere typen zodat dit het enige was dat aan het eind van de simulatie overbleef. Nadat we expliciete ruimte introduceerden, konden er wel verschillende typen samenleven. In deze expliciete ruimte waren er lokaal verschillen in dichtheid, doordat door toeval op de ene plek meer of minder zaad terechtkwam dan op andere plekken. In een andere simulatie vonden we al dat, met toenemende dichtheid, een type dat meer investeerde in hoogtegroei de sterkste concurrent was. Door de variatie in dichtheid vonden verschillende typen hoogte-investeerders af en toe goede omstandigheden om te groeien en konden ze zich handhaven in het ruimtelijke systeem.

In **hoofdstuk 5** hebben we de hoogtegroei voor alle planten constant gehouden. In plaats van op elk moment een deel van hun energie in de productie van zaad te steken, staken de planten nu alle energie eerst in de groei van vegetatieve delen om op een gegeven moment compleet over te schakelen en hun energie voor het produceren van zaden te gebruiken. De typen verschilden onderling in het tijdstip waarop ze al hun energie in reproductie investeerden. Als resultaat verschilden de types in de duur van de periode van vegetatieve groei en dus concurrentie-kracht. Wanneer alle typen met elkaar concurreerden, kregen we een successie van typen met lage concurrentie-kracht (maar hoge zaad-productie) naar typen met hoge concurrentie-kracht (maar weinig zaad-productie). Op een bepaald moment konden de uitgestorven typen weer in de vegetatie terugkeren, waardoor de successie tot in eeuwigheid doorging. Verschillende plantentypen konden dus samenleven, maar dit was wel min of meer gescheiden in de tijd.

In **hoofdstuk 6** zagen we, dat typen die verschilden in concurrentie-kracht ook gelijktijdig konden samenleven. Alhoewel de sterkere typen de zwakke typen onderdrukten waar ze deze tegen kwamen, waren er plekken in de vegetatie die niet door de sterke typen werden bezet. Dit kwam doordat de sterkere typen weinig zaad produceerden, en nog minder als ze elkaar tegenkwamen. Op deze manier bleef de dichtheid van de sterke soorten laag. Omdat zwakkere typen niet erg concurrentiekrachtig zijn, konden ze op een klein oppervlak een hoge dichtheid bereiken. Doordat deze vele kleine planten samen veel zaad konden produceren, konden ze de lege plekken goed

bereiken en zich in de vegetatie handhaven. Typen met een middelmatige concurrentiekracht lieten geen open plekken in de vegetatie over. Als we het systeem lieten evolueren, evolueerde elk type uiteindelijk naar het sterkste type. In combinatie met een sterk type, werden de middelmatig sterke typen in hun groei gehinderd, zodat er toch nog open plekken voor de zwakke typen bleven bestaan. Op deze manier konden er typen met verschillende concurrentiekracht met elkaar samenleven, ook al konden de individuele combinaties van typen vaak niet samenleven.

In **hoofdstuk 7** onderzochten we de manier waarop een plant zijn vorm kan gebruiken om de concurrentie te winnen. We vonden, dat planten hun groei konden verlengen door bladeren weg te gooien, vooral tegen het einde van de groei. Hierdoor reduceerde de plant zijn kosten om bladeren te onderhouden die toch al overschaduwd werden door het inmiddels geproduceerde bladerdek. Dit was alleen voordelig voor planten die niet met andere planten hoefden te concurreren. Voor planten onder competitie was het voordelig om blad te behouden. In een concurrentie-situatie bleek het voordelig om een hogere investering in hoogtegroeï te hebben dan de concurrenten. Het was ook voordelig om meer bladeren op hogere posities aan de stengel te hebben dan de concurrenten. Deze beide strategieën combineren was juist weer niet voordelig. Planten met een hoge concurrentiedruk konden, om de competitie te winnen, beter in de hoogte groeien dan hun bladeren naar hogere posities langs de stengel te verplaatsen.

NAWOORD

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CURRICULUM VITAE

Theresia Elisabeth Pronk was born on 2 March 1976 in Amersfoort, The Netherlands. From 1988 to 1994 she attended secondary school at the Eemland College in Amersfoort. After graduation, in 1994, she began her study Biology at Wageningen University. There she followed the Ecosystem specialisation, with a focus on Plant Ecology. During this study, three graduation projects were carried out. The first was an experimental study on the effects of root-feeding nematodes on the succession of grass species. This was carried out in the greenhouse. The second project consisted of a combination of fieldwork and modelling and was carried out in a fresh water swamp reserve in Israel. Together with a fellow-student she studied the effects of Buffalo-grazing on vegetation development. This specific study triggered an interest in modelling. The last project was to implement the model on the effect of grazing in a spatially explicit model environment. She attained her Msc. degree in September 1999. In January 2000 she started as a PhD at the Plant Ecology Group, Utrecht University. In this research she studied, with the help of computer modelling, the role of plant traits on the coexistence of plants. The resulting thesis you now have before you. In the coming year she will work for five months as a post-doc at the Plant Ecology group of Tohoku University, Sendai, Japan.

