

Plant traits in forest understory herbs - a modeling study -

Planteneigenschappen van kruiden op de bosvloer
- een modelleerstudie –

(met een samenvatting in het Nederlands)

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Plant traits in forest understory herbs

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*I try to testify that we live in a beautiful, orderly
world, and not in a formless chaos, as it so often seems.
M.C. Escher*

TABLE OF CONTENTS

Chapter 1	Introduction	1
Chapter 2	Modeling plant growth, biomass allocation and leaf functional traits (with Feike Schieving)	11
Chapter 3	Shade tolerance: the role of leaf functional traits and biomass allocation (with Feike Schieving)	55
Chapter 4	The role of plasticity in shoot-to-plant ratio under different light and nitrogen conditions	85
Chapter 5	Light, nutrients and the growth of herbaceous forest species: an experiment (<i>Acta Oecologica</i> , 26(3):197-202)	101
Chapter 6	Summary and general discussion	111
	Literature cited	121
	Nederlandse samenvatting	135
	Acknowledgements	143
	Curriculum Vitae	145

Chapter 1

Introduction

BACKGROUND

THE AFFOREST-PROJECT

A surplus of grain and other agricultural products has caused changes in the EU Common Agricultural Policy and substantial areas of agricultural land have been taken out of production. Much of this land is suitable for afforestation. The governments of several EU countries have decided to actively promote an increase in the forest area to be planted on former farmland within the next decades in order to contribute to the removal of greenhouse gases from the atmosphere. Afforestation is a shift in land use that may have significant effect on the environment. An uncertainty in the governmental decisions is what environmental aspects will be affected and to what extent. The EU-project AFFOREST is set up to evaluate the impact of afforestation practices on environmental factors. Four environmental categories have been selected: carbon sequestration, atmospheric deposition, leaching of nitrate, and groundwater recharge. The fifth focus of the AFFOREST-project, the developmental possibilities of the understory vegetation on previously cultivated land, resulted in this thesis. The main focus of this study is on the effects that environmental factors have on the growth processes of the (understory) species.

THE FOREST ENVIRONMENT

Forest ecosystems, both old-growth and recently planted on former agricultural land, can be characterized by the low availability of light reaching the understory vegetation for at least part of the growing season. In the course of the development of the forests, the light availability on the forest floor changes from relatively high in the first phase, although luxuriant growth of weedy species may intercept a large amount of light, to extremely low as the tree layer closes. Later in the development of the forest, when management is applied or natural thinning occurs, light availability increases again but still often remains below 10% of the light availability above the forest canopy. Not surprisingly, light is often mentioned as the most important factor limiting growth in the field layer. In many natural forest systems, except those growing on naturally rich soils, growth of the forest is also limited by nitrogen availability (Ash & Barkham, 1976; Barkham, 1992; Brewer, 1980, Brunet *et al.* 1997; Lameire *et al.*, 2000).

In forests planted on abandoned agricultural land large differences in nitrogen availability are expected compared to old-growth forest. The AFFOREST literature review (Hansen, 2002) summarized the development of nitrogen availability in forests on former agricultural land as follows: after afforestation the soil properties of the former arable land are slowly modified towards conditions found in closed forests. In the initial phase of afforestation high soil N contents, inherited from agricultural fertilization practices, support a continued high mineralisation and nitrification in the mineral soil. Even a century after afforestation, potential nitrification rates are higher in plantations on former cropland as compared to old forest soils. Besides differences in nitrogen availability, other nutrients are also expected to be in higher supply in those plantations.

Furthermore, pH in recent forests differs from that in ancient forests. Due to liming practices, agricultural soils are characterized by a high pH (neutral to weakly acid). Afforestation of arable land leads to a decrease in soil pH. The pH value of the new forest is largely determined by the rate of acid input, production and leaching in relation to the buffering capacity of the soil. The reduction in pH in the afforested soils is pronounced already after only a few years, indicating that the process is rather rapid (Hansen, 2002). Based on this information, in combination with the importance of light and nitrogen availability for plant growth, light and nitrogen availability have been selected as the environmental factors of focus in this study.

THE FOREST UNDERSTORY VEGETATION

The development of the forest understory of recently planted forests and the differences with so-called ancient forest systems have not often been subject to study. Still, some general trends and patterns can be described. To begin with, no consistent differences in species richness were found between the field layers of ancient and recent forests. However, the species composition of the field layers was found to differ considerable (e.g. Dzwonko, 2001; Hermy *et al.* 1999; Petersen, 1994; Petersen & Philipp, 2001; Singleton

et al., 2001). In general, in recent forests a larger share of fast-growing, nitrophilic species is present and species typical of the understory of old-growth forests, often named ancient forest species, are missing in the understory of recent forests.

As the major causes of the absence of ancient forest species in recent forests the limited dispersal abilities, low amounts of diaspore production and recruitment problems of those species have been brought forward (Hermy *et al.*, 1999). Many forest species produce only a few large seeds and the dispersal mechanism is specialized for short-distance dispersal (Bierzychudek, 1982; Brunet & von Oheimb, 1998; Hermy *et al.*, 1999). Hence, the absence of these species from the recent forest understory cannot be simply attributed to the direct or indirect consequences of increased nitrogen availability, since it may very well be that the seeds of these species have not yet reached the new forest. Furthermore, the forests subject to those studies were mostly planted on land abandoned before the significant increase in application of artificial fertilizers in agricultural practice after World War II. Consequently, the availability of nitrogen in these forests will probably not have reached such excessive levels as occurred in forests planted on land that was more recently taken out of agricultural production.

Apart from dispersal, two other chains of processes determine the presence or absence of a species in a certain habitat: physiological capability of survival in the environment, and biotic interactions (Lambers *et al.*, 1998). The increased nitrogen availability in forests planted on former agricultural land may increase the intensity of biotic interactions and bring about an advantage for competitive species as has been shown for many other ecosystems (e.g. Heil & Bruggink, 1987; Willems *et al.*, 1993). However, in the forest understory, the constraints of low light conditions on growth may be sufficient to mask all effects of differences of nutrient availability (Lameire *et al.*, 2000b; Meekings & McCarthy, 2000).

Several studies have addressed the effects of increased nitrogen deposition on the understory vegetation of existing old-growth forests. Most studies report an increase in the number and cover of those species that are generally considered to be N indicators in the forest floor vegetation (Brunet *et al.*, 1998; Diekmann *et al.*, 1997, 1999; Lameire *et al.*, 2000; Thimonier *et al.*, 1992, 1994; Van Dobben *et al.*, 1999). The species' ecological indicator values in these studies are determined on the basis of Ellenberg's indication values for nitrogen availability or based on literature citations on the nitrogen demand of the species. Kirby & Thomas (2000) found no evidence for an effect of changing soil N levels on the vegetation composition. In the Witham woods in Southern England, species with high Ellenberg scores for nitrogen availability were found both among the species that increased and those that decreased between 1974 and 1991. On the fate of species characteristic for a natural forest understory vegetation, the studies report less extensively. In general it is assumed that these species decline as a consequence of either the direct or indirect effect of increased nitrogen availability. Although there were indications that the described changes in vegetation composition may have been partly affected by light availability, none of the studies have involved this factor in their measurements and analysis.

Before predictions can be made of development of a valuable forest understory or an assessment can be made of the possibilities for non-forest species to invade the forest interior the growth processes in the understory environment have to be understood. Thereto a plant ecological approach, focusing on the interaction between plant traits, environmental factor and growth processes, can be followed. The first step is in this process is to select key plant traits and determine how different species groups, from old-growth and recent forests, differ in those.

PLANT ECOLOGICAL APPROACH

PLANT GROWTH STRATEGIES

A fundamental and vital activity of plants is the uptake, processing, and allocation of resources from the environment (Bazzaz & Grace, 1997). Since plants are the product of natural selection a repeated encounter of specific environmental circumstances must have honed the process of allocation (Bazzaz & Grace, 1997). A myriad of processes of natural selection has led to species with different (suites of) traits that allow them to perform in specific habitats. So, differences among species in their intrinsic (suite of) traits and their plasticity may reflect interspecific microhabitat differentiation (Reich *et al.*, 1998b; Vonwillert *et al.*, 1990). Such a (suite of) traits is often referred to as a strategy (Lambers *et al.*, 1998).

The two main resources needed for plant growth, carbon and nitrogen, are acquired by two different plant compartments (above and belowground organs). The division of biomass between shoot and root determines the ratio in which the resources can be acquired and thus plays an important role in plant growth. The relative allocation to shoot, expressed as shoot-to-plant ratio, and the relative allocation to roots, root-to-plant ratio, has since long engaged plant ecologists. Another factor that has been brought forward as playing an important role in growth processes and that appears to differ strikingly between species is the allocation of leaf mass to leaf area, expressed as Specific Leaf Area (SLA).

SHOOT-TO-PLANT RATIO

Carbon and nitrogen needed for plant growth are acquired by, respectively, the above and belowground plant organs. Allocation of new biomass to either one of those compartments will enhance capture of the resource taken up by that compartment. However, biomass allocated to one compartment cannot be allocated to the other compartment, so enhancement of the capture of the one resource occurs at the cost of the relative uptake of the other resource. Furthermore, shoot and root biomass are interdependent: the shoots need the nitrogen taken up by the roots and the roots need the

carbohydrates produced in the shoot. Logically, the division of biomass between shoot and roots has large implications for total plant growth.

The functional equilibrium theory of biomass allocation states that plants respond to their environment in such a way as to optimize their resource acquisition (Brouwer 1962a, 1962b, 1963). When belowground resources are in short supply, the growth of the roots is favored over that of the shoot; when light is limiting growth, the opposite occurs. This theory is generally accepted and a number of studies report adjustments in biomass allocation consistent with it (reviewed in Bloom *et al.*, 1985).

Implicit in the model of the functional equilibrium is that a plant allocates its biomass in such a manner that its growth rate is maximal under the given environmental conditions (Poorter & Nagel, 2000). However, not all plants are equally capable of adjusting their shoot-to-plant ratio to their growing conditions. Large differences have been reported both between species and between species groups. Apparently, natural selection has not favored plasticity in all situations (Alpert & Simms, 2002).

The functional equilibrium theory has been formulated to explain plastic responses to changes in the plant's growing environment. Presuming natural selection has acted upon the inherent biomass distribution of species, selecting for the highest biomass production rate, it can be assumed that species adapted to different habitats will also differ in inherent shoot-to-plant ratio in accordance with the patterns described in the functional equilibrium theory.

SPECIFIC LEAF AREA

A large share of the research on Specific Leaf Area (SLA) has focused on the plastic response to different light and nutrient conditions found within a species. As for shoot-to-plant ratio, general trends can be described. A plant growing at low light conditions generally has a higher SLA than a plant from the same species growing at high light conditions (e.g. Baruch *et al.* 2000; Bungard *et al.* 1998; Evans & Poorter 2001; Meziane & Shipley 1999; Shipley 2000), SLA decreased when plants were moved to lower levels of nitrogen availability (e.g. Knops & Reinhart 2000; Li *et al.* 1999; Meziane & Shipley 1999). Although many species exhibit a similar plastic response, the extent to which they are plastic differs.

SLA has also been described in relation to a set of correlated leaf functional traits. Based on physiological, morphological and biomechanical constraints a trade-off has been described between the acquisition of carbon by the leaves and the conservation of acquired carbon. On the extreme ends of the trade-off spectrum two strategies can be distinguished: a plant can either produce leaves that possess a high photosynthetic assimilation rate with high maintenance costs and that persist briefly, or provide a resistant leaf physical structure with lower photosynthetic capacity and a smaller light capturing area per gram of leaf dry mass (SLA) resulting in a lower carbon assimilation rate but over a longer period of time (Reich *et al.*, 1992). The underlying explanation for the trade-off is that high photosynthetic rates require a high leaf nitrogen concentration to

enable the construction of a large photosynthetic complex. The periodic (and costly) re-synthesis of the enzymes of this photosynthetic complex requires a large share of respiration costs. Furthermore, SLA has been shown to be positively correlated to the loss of leaf biomass in a variety of habitats (Reich *et al.*, 1992, 1997; Westoby *et al.*, 2000). Low-SLA leaves generally are thicker, physically more tough and tend to have larger amounts of secondary chemical defenses (Ninnemets, 1999; Westoby *et al.*, 2000, 2002; Wilson *et al.*, 1999) and thus have a lower loss rate. The relations between the different components of the suite of correlated leaf functional traits have been described based on statistical analysis of leaf trait data spanning a large amount of species from different biomes on a global scale (Wright *et al.*, 2004).

SHADE TOLERANCE AND GROWTH UNDER LOW LIGHT CONDITIONS

In plant ecology, it has been hypothesized that a set of leaf and plant level attributes, such as leaf life span, Relative Growth Rate (RGR) and SLA vary systematically among species adapted to high versus low resource habitats (Reich *et al.*, 1998b). Until recently, the fundamental assumption that shade-tolerant species possess enhanced carbon-capture abilities, suitable to support fast growth under conditions of low light intensity had persisted (Walter & Reich, 1999). However, no evidence of low-light growth advantages for tolerant species have been found. In their review of the low-light carbon balance of the seedlings of woody plants Walters & Reich (1999) found a trade-off between growth potential and low light survival. They suggest that this trade-off can be attributed to the combination of a stronger selection on energy conservation traits if the RGR is severely constrained by low light, and direct selection against high, and unused, growth capacity in low light, if excess capacity directly promotes greater energy or biomass loss rates via higher rates of respiration, tissue turnover, mechanical damaging and herbivory. Integration of this hypothesis with the above-described set of correlated leaf traits, which can be represented by SLA, leads to the hypothesis that typical shade-tolerant species should have a high SLA. This is consistent with the conclusions of the review of Walters & Reich (1999). Their data clearly demonstrated that young seedlings of shade-tolerant species do not possess higher SLA and do not achieve higher net carbon gain than shade-intolerant species. The same result was found in a study on the growth of tropical tree seedlings in contrasting light environments (Veneklaas & Poorter, 1998), but an extensive and structural study of this hypothesis has so far not been conducted.

It has been hypothesized that species from low-resource habitats may be less plastic (Alpert & Simms, 2002; Dong *et al.*, 1996; Grime & Mackey, 2002). This is attributed to the costs of plasticity that, under low resource availability, may not be offset by the advantages of plasticity. Costs may be involved in maintenance and production of the sensory mechanisms, plasticity genes, developmental instability, information acquisition and assessment of the environment (DeWitt *et al.*, 1998; Huber *et al.*, 1998). Moreover, plasticity in morphological plant traits, like shoot-to-plant ratio and specific leaf area,

involves the costs of production, shedding and replacement of plant parts with different characteristics (Grime & Mackey, 2002). However, there is little empirical support for a relationship between resource levels and plasticity (Alpert & Simms, 2002).

Another aspect that is brought forward in the discussion on the relation between environment and plasticity is the variation in resource availability and the contrast between different states. Variation in resource availability should favour high plasticity. However, if the contrast is too high, plastic adaptation to one state can create severe resource limitation after conditions have changed. In the understory of a deciduous forest a highly predictable, steep decrease is found in the first phase of the growing season. The allocation pattern followed in the high light phase of the growing season and the accompanying biomass production will have consequences for growth and the steering possibilities as light conditions have deteriorated. Under these circumstances a high plasticity may not be favourable.

Although many ideas exist about the traits that characterize shade-tolerant species from the forest understory, so far no clear and comprehensive definition can be given. However, research into plant characteristics that play an important role in growth under different light conditions provided useful insight into the set of mechanisms that may be underlying differences in species groups from different environmental conditions. This set of mechanisms is used in this study to evaluate existing hypotheses regarding shade-tolerance.

MODELING APPROACH

In the systematic analysis of the role of plant traits in growth processes mechanistic models can provide a valuable contribution. A model system allows the isolation of a specific trait or suite of traits in order to study its relation with environmental factors and plant growth processes. A mechanistic approach can thus be used to test plant ecological hypotheses and to provide explanations for observed patterns. Once the role of one (suite of) trait(s) is understood, the interaction with other plant traits or the role of plasticity in that trait can be addressed.

Already quite a large number of models, predicting allocation patterns or the effect of specific plant traits on growth, are available. However, not in all these models growth processes are based on mechanisms but instead steered by (a set of) growth and allocation rules. These models can only be used to analyze and predict allocation patterns in circumstances for which the model has been developed but cannot be extended to conditions for which the plant has not been calibrated. Furthermore, most of the models assume exponential growth. These models (analytically) determine the constant growth rate, shoot-to-plant ratio and internal carbon and nitrogen availability in the steady state situation. In this type of models the effect of feedback-mechanisms and self-shading processes are not taken into account. Consequences of changes in the plant over time are

thus not taken into account, despite of their effect on the resource demand of the plant. Due to these constraints, the existing models are not suitable for realistically simulating growth under new and uncharted conditions and cannot be used to analyze interactions between different plant strategies.

In this study a mechanistic plant growth model is presented, building on the work of Schieving (1998), simulating acquisition and allocation of carbon and nitrogen. It includes a simple but realistic light environment in which light extinguishes with depth in the canopy. It also includes the establishment of a nitrogen gradient in the soil that is affected by the activity and size of the root biomass. The model offers the possibility to define different species in terms of biomass allocation pattern, leaf functional traits and levels of plasticity. The mechanism of plastic biomass allocation is driven by the ratio of the internal carbon and nitrogen concentrations and aims at maximization of the biomass production over a certain time period. The model can be used to assess the optimal trait combinations in different light-nitrogen environments. It can also be used to evaluate the role of plasticity for performance in different environments. The model can be extended to a competition model to evaluate the effect of those plant traits when resources have to be shared.

OUTLINE OF THIS THESIS

The aim of this thesis is to study the role of (plasticity in) shoot-to-plant ratio and leaf functional traits in plant growth processes under different environmental conditions. Special focus is put on the plant traits that enable survival and growth in low-light conditions. Once the intrinsic traits of different species groups have been characterized, the effect of changing environmental conditions on species interactions can be assessed. Initially, the problem is approached using a mechanistic plant growth model, described in Chapter 2. This model has been designed to simulate the biomass production of species differing in leaf functional traits and shoot-to-plant allocation pattern. Besides the model description, an illustration of the general model behavior is given in this chapter. The model offers possibilities for an extension to a competition model.

In Chapter 3, the consequences of the correlation between leaf functional traits are tested under different light availabilities. Model plants are set to differ in SLA, defining their position in the spectrum of the trade-off between carbon gain and conservation of biomass and energy. The hypothesis that under low light conditions a conservation strategy may be more profitable in terms of net biomass production, while under high light conditions a high-gain-high-turnover strategy favors high biomass production, is tested. Furthermore, the consequences of differences in shoot-to-plant ratio for growth under different environmental conditions are evaluated. The pattern of optimal shoot-to-plant ratio in different environments is expected to comply with the functional equilibrium theory of (plastic) biomass allocation.

Chapter 4 addresses the question whether plants generally occurring in the forest understory should be plastic in their biomass allocation or if a more rigid allocation pattern is more favorable. By analyzing the biomass production of model plants following a different allocation strategy this question is answered.

In Chapter 5 the differences in shoot-to-plant ratio and Specific Leaf Area between forest species and species from the forest edge is studied in an experiment. Four different species, two from each group, were grown at different levels of light and nutrient availability and their characteristics were described. The results can be tested against the predictions of Chapters 3 and 4.

Finally, in Chapter 6, the results of the earlier chapters are summarized and discussed. Furthermore, based on the characterization of the species adapted to low light conditions and species better suitable to grown under high light conditions, vegetation processes in the forest understory are discussed as well as the effect of increased nitrogen availability on the competition between the two species groups.

Chapter 2

Modeling plant growth, biomass allocation and leaf functional traits

ABSTRACT

Recent studies report that nowadays non-forest species penetrate evermore in the forest understory while a decline in the abundance of typical forest species is found. Important factors in plant growth in the understory of both recent and ancient forests are light and nitrogen availability. There are two major species traits, shoot-to-plant ratio and Specific Leaf Area, that have been recognized as important in de specialization and acclimation to different light and nutrient conditions and may thus play a role in the shift in species composition. Modeling provides a suitable method to asses the role of these plant traits in plant performance in relation to light and nutrients. Up to now, efforts to model the biomass partitioning to shoot and roots have mainly addressed plastic allocation patterns of plants increasing exponentially in biomass. In this study, a mechanistic plant growth model is presented that includes the logistic growth phase with accompanying realistic photosynthesis and N uptake processes. The model offers the possibility to define different species in terms of biomass allocation, leaf functional traits and levels of plasticity and can be used to assess the optimal trait combinations in different light-nitrogen environments. Besides a detailed description of the model, an illustration of the general behavior of the model is given. The results showed a realistic biomass production and an expected effect of resource level. Furthermore, the simulations demonstrated that the transition from exponential growth to logistic growth had consequences for the acquisition and demand of carbon and nitrogen changed and for the allocation processes in the plastic plant.

Keywords: leaf functional traits, light, logistic growth, mechanistic plant growth model, nitrogen, shoot-root allocation.

INTRODUCTION

Vegetation science has extensively documented that certain species are found growing together in certain locations and environments more frequently than would be expected by chance (Braun-Blanquet, 1964; Kent & Coker, 1992; Whittaker, 1975). Specialized species communities have also been described for the forest understory and the forest edge (Stortelder *et al.*, 1999; Westhoff & Den Held, 1969). Such a species composition results from three different processes: dispersal, physiological capability of survival in the environment, and biotic interactions (Lambers *et al.*, 1998). Since there is no reason to assume that species generally occurring in the forest edge or outside the forest are dispersal limited, the absence of these species within the forest interior is probably caused by the other two processes.

Recent studies report that nowadays non-forest species penetrate evermore in the forest understory of both recent and ancient forests while a decline in the abundance of typical forest species is found (Harmer *et al.*, 2001; Lameire *et al.*, 2000). This raises the questions: what are the processes and mechanisms that cause this phenomenon, and which plant traits play an important role?

It has been hypothesized that the driving force behind the shift in species dominance is increased nitrogen availability (Brunet & von Oheimb, 1998b; Diekmann *et al.*, 1999, 1997; Lameire *et al.*, 2000; Thimonier *et al.*, 1992, 1994; Van Dobben *et al.*, 1999). Different species groups, i.e. typical shade-tolerant forest species and fast-growing species from better lit sites in the forest edge, are assumed to react differently to an increased nitrogen supply. Furthermore, light availability, which is generally low on the forest floor, may interact with nitrogen supply in its effect on plant performance.

There are two major species traits, shoot-to-plant ratio and Specific Leaf Area (Lambers *et al.*, 1998), that have been recognized as important determinants of plant performance. These plant traits are described as important in the specialization and acclimation to different light and nutrient conditions and may thus play a role in the shift in species composition.

Part of the research on shoot-to-plant ratio has focused on inherent differences in allocation strategy between species. Species adapted to different environments tend to possess different shoot-to-root ratios (Aerts, 1994; Berendse & Elberse, 1989; Olff *et al.*, 1990; Tilman 1985; but see Körner 1991). Other studies have dealt with the plastic response of species' shoot/root ratio to environmental conditions. This line of research is based on the functional equilibrium theory (Bloom *et al.*, 1985; Brouwer, 1962a,b, 1963) that states that plants respond to their environment in such a way as to optimize their resource acquisition. Plasticity in allocation patterns within species is expected to be smaller than inherent differences in shoot/root ratio between species (Tilman, 1988). The same distinction in research focus can be made for the research on Specific Leaf Area (SLA). Interspecific differences in SLA have been described as part of a set of correlated traits related to carbon economics, viz. leaf life-span, photosynthetic capacity (A_{mass}), leaf

Introduction

nitrogen (N_{mass}) and dark respiration rate (Kikuzawa, 1995; Reich *et al.*, 1998b; Westoby *et al.*, 2002; Wright *et al.*, 2004). Within species a plastic response to light has been found. In general a species grown at low light conditions tends to have leaves with a higher SLA than the same species grown at higher light conditions (Bungard *et al.*, 1998).

Modeling provides a suitable method to assess the role of these plant traits in plant performance in relation to light and nutrients. A model offers the possibility to divide the problem into separate sub-problems and allows a considerable simplification of the research system, thus enabling a stronger focus on the role of specific plant characteristics and, more importantly, on the interactions between these characteristics. This then can contribute to a better understanding of the plant ecological mechanism behind an observed shift in species distribution.

Up to now, efforts to model the biomass partitioning to shoot and roots have mainly addressed plastic allocation patterns of plants increasing exponentially in biomass. The shoot-to-plant ratio of an exponentially growing plant eventually achieves a steady state situation and does not change any more. This simplifies the analyses and enables a clearer understanding of the basic relationship between partitioning and resource availability (Dewar, 1993).

When following a teleonomic approach, supposing maximization of the biomass production of the plant over its life-time, processes of self-shading and increased root density may affect the resulting optimal biomass partitioning between shoot and root. Development of a model that includes the logistic growth phase with accompanying realistic photosynthesis and N uptake processes therefore will be a valuable addition to the arsenal of biomass partitioning models.

In this study a mechanistic plant growth model is presented, building on to work of Schieving (1998), simulating acquisition and allocation of carbon and nitrogen. It includes a simple but realistic light environment in which light extinguishes with depth in the canopy. It also includes the establishment of a nitrogen gradient in the soil that is affected by the activity and size of the root biomass. The model offers the possibility to define different species in terms of biomass allocation pattern, leaf functional traits and levels of plasticity. The mechanism of plastic biomass allocation is driven by the ratio between the internal carbon and nitrogen concentrations and aims at maximization of the biomass production over a certain time period. The model can be used to assess the optimal trait combinations in different light-nitrogen environments. It can also be used to evaluate the role of plasticity for performance in different environments. The model can be extended to a competition model to evaluate the effect of those plant traits when resources have to be shared.

In this chapter a detailed description of the model is given as well as an illustration of the general behavior of the model plant.

MODEL DESCRIPTION

THE BASIC SYSTEM

The model presented in this chapter represents a mechanistically growing annual plant driven by carbon (carbohydrates) and nitrogen (amino acids). Several plant variables are important in the description of the status and dynamics of the model plant. The basic system is described by total plant mass M_p , shoot-to-plant ratio σ and carbon and nitrogen concentration in the substrate pool, represented by c and n respectively. A list of abbreviations and units is given in Table I.

The total plant mass M_p reflects the net growth of the plant from the start of the simulation. It is used to assess the performance of the plant. The total plant mass is built up of structural carbon and nitrogen. It performs two different functional tasks, the acquisition of carbon and the uptake of nitrogen. Therefore it is divided into aboveground biomass M_a , responsible for carbon acquisition, and belowground biomass M_b , involved in nitrogen uptake ($M_p = M_a + M_b$), all expressed in gram dry weight.

Above and belowground biomass are depicted as homogeneously distributed biomass within an above c.q. belowground cylinder with a fixed diameter that can expand in height (Figure 1).

The shoot-to-plant ratio σ ($\sigma = M_a/M_b$) represents the distribution of biomass over the two compartments. Above and belowground biomass is further divided into functional biomass, i.e. leaves and fine roots, and supportive biomass, i.e. stems and coarse roots. Leaves represent productive photosynthetic tissue and fine roots are responsible for the uptake of nitrogen. Stem and coarse root biomass provide support to the functional biomass and represent costs associated with height expansion of the plant. Supportive biomass does not directly contribute to the acquisition of resources. The allocation pattern between functional and supportive biomass changes with height, as will be described in more detail in the section on the division of above and belowground biomass.

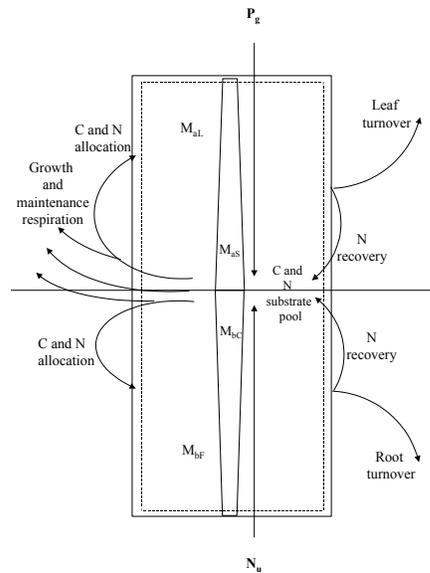


Figure 1 Schematic representation of the model structure and the most important processes involved in the growth of the plant. M_{aL} is the aboveground leaf mass, M_{bF} the belowground fine root mass, M_{aS} and M_{bC} are the supportive stem and coarse root mass respectively, P_g is the gross photosynthetic carbon gain rate and N_u is the nitrogen uptake rate. The substrate pool, defined as a uniformly distributed pool of available substrate within the total biomass of the plant, is represented here schematically as a separate compartment within the plant and is indicated by the dashed line.

Model description

Carbon and nitrogen acquired in photosynthesis and nitrogen uptake are first stored in a substrate pool. The carbon and nitrogen in this pool represent a stock of substrate available for growth and maintenance. This substrate is freely available for investment in either above or belowground biomass. Transport costs, which are supposed to take place on a finer time scale than used in this model, have not been included in the model. In Figure 1 the substrate pool is represented schematically as a separate compartment within the plant but it is implemented in the model as a uniformly distributed pool of available carbon and nitrogen substrate within the total structural biomass of the model plant. The mass represented by the carbon and nitrogen pools are not included in the total biomass M_p , however. The carbon and nitrogen concentrations in the substrate pool, c and n respectively (in gram per gram), play an important role in growth and allocation of the model plant as will become clear from the description of the growth and allocation processes in the next sections. These concentrations are defined as:

$$C \text{ concentration} \quad c = \frac{C}{M_p} \quad (1)$$

and:

$$N \text{ concentration} \quad n = \frac{N}{M_p} \quad (2)$$

with C and N (in gram) the total amount of carbon or nitrogen respectively available in the substrate pool in gram.

DYNAMICS OF THE BASIC SYSTEM

The dynamics of the basic plant system are described as the change over time in the plant variables described above.

The net growth rate dM_p/dt is the result of the relative biomass production rate μ_p and the relative biomass loss rate τ_p , both in gram plant mass per g plant mass per day, i.e.:

$$Plant \text{ growth rate} \quad \frac{dM_p}{dt} = M_p (\mu_p - \tau_p) \quad (3)$$

Since total biomass consists of aboveground and belowground biomass, the production and loss of total plant mass can also be described in terms of the production and loss rates of above and belowground biomass, $M_a(\mu_a - \tau_a)$ and $M_b(\mu_b - \tau_b)$ respectively. The relative aboveground production and loss rates, μ_a and τ_a respectively, are expressed as gram aboveground plant mass per gram aboveground plant mass per day and, similarly, the relative belowground production and loss rates, μ_b and τ_b , are expressed in gram

Table I List of abbreviations and units

Abbreviation	Meaning	Unit
M_p, M_a, M_b	Total, aboveground or belowground plant mass	g
MaL, MaS	Functional and supportive aboveground plant mass	g
MbR, MbS	Functional and supportive belowground plant mass	g
σ	Shoot-to-plant ratio	-
c, n	Carbon or nitrogen concentration in the substrate pool	$g\ g^{-1}$
C, N	Total amount of carbon or nitrogen in the substrate pool	g
μ_p, μ_a, μ_b	Relative production rate of total, aboveground or belowground mass	$g\ g^{-1}\ d^{-1}$
$\mu_p^{cap}, \mu_a^{cap}, \mu_b^{cap}$	Relative production capacity of total, above or belowground mass	$g\ g^{-1}\ d^{-1}$
τ_p, τ_a, τ_b	Relative loss rate of total, aboveground and belowground mass	$g\ g^{-1}\ d^{-1}$
p_g	Gross photosynthetic rate	$g\ g^{-1}\ d^{-1}$
r_m, r_{nu}	Respiration rate demanded in maintenance or nitrogen uptake	$g\ g^{-1}\ d^{-1}$
u_n	Nitrogen uptake rate	$g\ g^{-1}\ d^{-1}$
c_c, n_c	Carbon or nitrogen construction cost for new biomass	$g\ g^{-1}$
n_r	Nitrogen that can be retrieved from shed biomass	$g\ g^{-1}$
ϕ	Allocation ratio	-
u_r, Max, α	Parameters of allocation control function	-
$f(c,n)$	Substrate availability factor	-
k_c, k_n	Semi-saturation constants of substrate availability equation	-
c_{min}, n_{min}	Carbon or nitrogen concentration at which growth stops	$g\ g^{-1}$
c_{leth}, n_{leth}	Carbon or nitrogen concentration at which plant is declared dead	$g\ g^{-1}$
LL	Leaf longevity	d
k	Constant of the τ -LL relation	-
SLA, SRA	Specific Leaf Area, Specific Root Area	$m^2\ g^{-1}$
a_L, b_L	Parameters of the SLA-LL relation	-
P_{Ma}, P_{MaL}, P_{MaS}	Absolute production rates of Ma, MaL or MaS	$g\ d^{-1}$
r_{ac}, r_{bc}	Radius of the above or belowground cylinder	m
ρ_{MaL}, ρ_{MbR}	Density of leaf mass in the cylinder	$g\ m^{-3}$
H_{ac}, H_{bc}	Height of the above or belowground cylinder	m
k_H, β	Parameters of the height – stem mass relation	-
$i(h), i_0$	Light intensity at height h or directly above the plant cylinder	$\mu mol\ C\ m^{-2}\ s^{-1}$
a_L	Absorption coefficient of the leaves	-
α_L	Inclination of the leaves in relation to the horizontal plane	rad
F, F(l)	Total leaf area of the plant or of layer	m^2
$i_{at}(h)$	Light interception of leaves at height h	$\mu mol\ C\ m^{-2}\ s^{-1}$
P_{gml}, P_{gl}	(Maximum) Photosynthetic rate	$\mu mol\ CO_2\ m^{-2}\ s^{-1}$
Φ	Quantum yield per unit absorbed light	$\mu mol\ CO_2\ \mu mol^{-1}$ photons
θ	Curvature factor of the photosynthesis – light relation	-
$P_g, P_g(l)$	Gross photosynthetic carbon gain rate of plant or of layer	$g\ d^{-1}$
F_p, F_{nu}	Feedback factor on P_{gml} or N_u^{cap}	-
n_a, n_{cy}, n_{dz}	Nitrogen concentration in the ambient soil, the rooting cylinder or the depletion zone	$g\ m^{-3}$
R_{nc}, R_{nd}	Resistance for nitrogen transport in the soil	$d\ m^{-1}$
N_u^{cap}	Nitrogen uptake capacity	$g\ d^{-1}$
N_u	Nitrogen uptake rate	$g\ d^{-1}$
k_{nd}	Semi-saturation constant for nitrogen uptake capacity	-
p, p _n	Parameters of the feedback factor equations	-

Model description

belowground plant mass per gram belowground plant mass per day. The production and loss rates per unit plants mass are related to the production and loss rates per unit shoot and root mass by:

$$\text{Biomass prod. rate} \quad \mu_p = \sigma \cdot \mu_a + (1 - \sigma) \cdot \mu_b \quad (4a)$$

$$\text{Biomass loss rate} \quad \tau_p = \sigma \cdot \tau_a + (1 - \sigma) \cdot \tau_b \quad (4b)$$

In the next sections, the determination of biomass production and loss rates will be described in more detail.

The growth rates above and belowground depend on the shoot-to-plant ratio σ . The rate of change of σ is a function of the change of aboveground biomass relative to the change of the total plant biomass. Using Equation 4a and 4b this rate of change can be written as:

$$\begin{aligned} \text{Change in } \sigma \quad \frac{d\sigma}{dt} &= \frac{d(M_a/M_p)}{dt} = \frac{1}{M_p^2} \cdot \left(\frac{dM_a}{dt} \cdot M_p - M_a \cdot \frac{dM_p}{dt} \right) \quad (5) \\ &= \frac{1}{M_p^2} \cdot (M_a \cdot (\mu_a - \tau_a) \cdot M_p - M_a \cdot M_p \cdot (\mu_p - \tau_p)) \\ &= \sigma \cdot ((\mu_a - \tau_a) - (\sigma \cdot (\mu_a - \tau_a) + (1 - \sigma) \cdot (\mu_b - \tau_b))) \\ &= \sigma(1 - \sigma) \cdot ((\mu_a - \tau_a) - (\mu_b - \tau_b)) \end{aligned}$$

In the same way, the equation of the change in C and N concentration can be derived; below the resulting equations are given. The rate of change of the carbon concentration in the substrate pool is determined by the outflow of carbon used in growth and respiration processes and the inflow of carbon acquired in photosynthesis. Furthermore, the carbon concentration in the substrate pool is subject to dilution and condensation due to a change in M_p , which is defined as the container of the substrate pool. So,

$$\text{Change in } c \quad \frac{dc}{dt} = \sigma \cdot p_g - r_m - r_{nu} \cdot (1 - \sigma) \cdot u_n - (c_c + c) \cdot \mu_p + c \cdot \tau_p \quad (6)$$

Where p_{mass} is the gross photosynthetic rate in gram carbon per gram total aboveground mass per day, r_m the maintenance respiration rate in gram carbon per gram plant mass per day, r_{nu} is the respiration demand in gram carbon per gram nitrogen, u_n is the nitrogen

uptake rate in gram nitrogen per gram dry weight per day, c_c is the carbon construction cost for new biomass in gram per gram new biomass and includes both the carbon investment of new structural biomass and the growth respiration costs needed for the production of this new structural biomass. $\sigma \cdot p_g$, r_m and $(1-\sigma) \cdot u_n$ are rates per unit plant mass. The dilution effect of an increasing plant mass, which is defined as the container of the substrate pool, is represented by $c \cdot \mu_p$ and the condensation effect of a decreasing container by $c \cdot \tau_p$. So, shed plant parts do not contain substrate pool elements. The calculations of the photosynthetic rate and nitrogen uptake rate are dealt with in later sections.

The dynamics of the nitrogen concentration in the substrate pool are handled analogously to the dynamics of the carbon concentration. The change in nitrogen concentration results from the inflow of nitrogen acquired in uptake and reallocation processes and outflow of nitrogen to growth processes (increase of M_p). Similar to the change in carbon concentration, inflow and outflow are expressed relative to the total plant mass. So,

$$\text{Change in } n \quad \frac{dn}{dt} = (1-\sigma) \cdot u_n - (n_c + n) \cdot \mu_p + (n_r + n) \cdot \tau_p \quad (7)$$

with n_c the nitrogen invested in newly produced biomass in gram nitrogen per gram new biomass and n_r the nitrogen that can be retrieved from senescent and later shed biomass in gram nitrogen per gram shed biomass. Analogous to Equation 6, $(1-\sigma) \cdot u_n$ is a rate per unit plant mass and the terms $n \cdot \mu_p$ and $n \cdot \tau_p$ represent respectively the dilution and concentration effect of the nitrogen concentration in the substrate pool due to production and loss of biomass.

THE PRODUCTION AND ALLOCATION OF BIOMASS

The maximum relative growth rate μ_p^{cap} of the total plant is divided into the relative growth capacity of the aboveground compartment μ_a^{cap} and the relative growth capacity of the belowground compartment μ_b^{cap} . Similarly to Equation 4a and 4b it can be written as:

$$\text{Plant growth capacity} \quad \mu_p^{cap} = \sigma \cdot \mu_a^{cap} + (1-\sigma) \cdot \mu_b^{cap} \quad (8)$$

The maximum relative growth rate of the total plant is supposed to be constant; the maximum relative aboveground and belowground growth rates are not. The partitioning between above and belowground growth capacity can be expressed as φ and by changing this parameter the plant can control its allocation pattern, i.e.

$$\text{Allocation ratio } I \quad \varphi = \frac{\mu_a^{cap}}{\mu_b^{cap}} \quad (9)$$

Control of the allocation can be considered as a means to adjust the distribution of biomass in such a way that the concentrations in the substrate pool are balanced and correspond to the demand for C and N imposed by growth and respiration processes. Thus, following this definition, the necessity to steer allocation depends on the ratio between the nitrogen and carbon concentrations in the substrate pool. If nitrogen availability in the substrate pool is high compared to carbon availability, plant growth is limited by carbon. Accelerating the growth of the aboveground compartment, obviously at the cost of the growth of the belowground compartment, can decrease this growth limitation. If the carbon concentration in the substrate pool is high in relation to the nitrogen concentration, plant growth is limited by nitrogen, and the opposite reaction will decrease nitrogen limitation.

An appropriate function to describe a continuous mechanistic allocation pattern exposing this behavior is the hyperbolic-tangent function. It is an anti-symmetric function, thus independent of parameter expression, that operates between certain boundaries (-1 and 1) and which can be set so that allocation is aimed at the n/c ratio the plant is supposed to maintain in the substrate pool (v_{ref}). Furthermore, the steepness of the response can be set. For this purpose the scaling factor α is introduced.

The hyperbolic-tangent function for allocation control is defined as:

$$\text{tanh-function} \quad y' = \tanh x' \quad (10)$$

$$\text{with} \quad y' = \frac{y}{\log(Max)}$$

$$x' = \frac{x}{\alpha}$$

$$\text{and:} \quad y = \log \varphi$$

$$x = \log(v_r)$$

The parameter v_r reflects the actual n/c ratio v relative to the optimal n/c ratio or reference ratio v_{ref} .

$$\text{Relative to optimal n/c} \quad v_r = \frac{v}{v_{ref}} \quad (11)$$

The definitions of y' , x' , y and x in Equation 10 can then be used to rewrite the *tanh*-function.

$$\frac{\log \varphi}{\log(Max)} = \tanh\left(\frac{\log v_r}{\alpha}\right) \quad (12)$$

$$\log \varphi = \log\left(Max^{\tanh\left(\frac{\log v_r}{\alpha}\right)}\right)$$

This then results in the equation of the allocation control parameter:

$$\text{Allocation ratio } \varphi = Max^{\tanh\left(\frac{\log v_r}{\alpha}\right)} \quad (13)$$

As can be seen in Figure 2, the above function produces values between 1/Max and Max and can be set so that allocation is aimed at the n/c ratio the plant is supposed to maintain in the substrate pool (v_{ref}). If the value of Max is set to one, the allocation control parameter equals one and the aboveground growth capacity equals the belowground growth capacity.

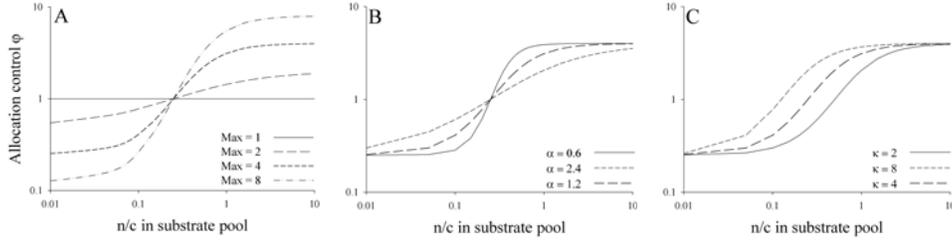


Figure 2 Shape of the allocation control function, reflecting the relation between n/c ratio in the substrate pool and allocation rates of biomass towards above and belowground biomass. The allocation control parameter φ is defined as the ratio between the aboveground growth rate and the belowground growth rate. Variation in parameter Max changes maximum and minimum ratio between the two growth rates (A), with the minimum value of Max=1 resulting in a straight horizontal line. Parameter α changes the slope of the curve (B) and parameter κ represents the n/c ratio at which the main direction of the allocation changes (C).

The allocation control parameter is used to determine the growth capacities of aboveground biomass and belowground biomass. They sum up to the constant total plant growth capacity μ_p^{cap} :

$$M_a \text{ growth capacity} \quad \mu_a^{cap} = \frac{\varphi}{(\sigma \cdot \varphi) + (1 - \sigma)} \cdot \mu_p^{cap} \quad (14)$$

$$M_b \text{ growth capacity} \quad \mu_b^{cap} = \frac{\mu_p^{cap}}{(\sigma \cdot \varphi) + (1 - \sigma)} \quad (15)$$

Model description

The growth rate of the plant can be limited by the availability of resources in the substrate pool. At high substrate availability the maximum growth rates μ_a^{cap} and μ_b^{cap} can be reached; when the supply of either one or both of the resources in the substrate pool is restricted, growth rate is slowed down. This limitation effect is described with a bi-substrate Michaelis-Menten equation that can be split up in a carbon availability factor (first term of the equation) and a nitrogen availability factor (second term).

$$\text{Substrate av. factor} \quad f(c, n) = \frac{(c - c_{min})}{k_c + (c - c_{min})} \cdot \frac{(n - n_{min})}{k_n + (n - n_{min})} \quad (16)$$

The parameters k_c and k_n can be regarded as semi-saturation constants, i.e. when c minus c_{min} equals k_c , half of the maximum growth rate is reached. A deficit of both substrates leads to a stronger growth limitation than when only one resource is in short supply (Figure 3). Growth stops as the carbon or nitrogen concentration reaches the value of either c_{min} or n_{min} . However, this does not guarantee that the concentrations cannot fall below this level. Especially the carbon concentration, which also serves as a pool for maintenance respiration, can still decrease even if the minimum concentration is reached. Therefore lethal concentration levels, c_{leth} and n_{leth} are introduced at which the plant is declared dead and its biomass is cleared away. Both carbon and nitrogen are equally available for growth of above- and belowground biomass. In other words, the growth rates of above- and belowground biomass are equally limited by carbon and nitrogen supply and thus Equation 5 can be used for both the above and belowground growth rates.

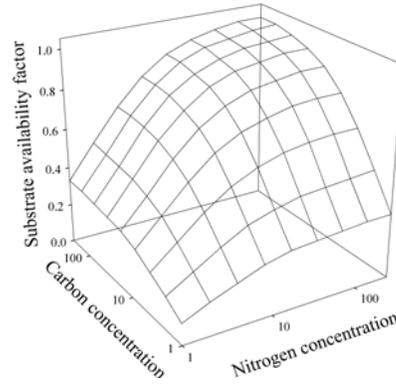


Figure 3 Visualization of the effect of resource supply in the substrate pool on the plant growth rate. The fraction of the growth capacity that can be realized, $f(c,n)$ is presented on the z-axis as function of the carbon and nitrogen concentrations presented on the other two axes.

The actual growth rates of above and belowground biomass are calculated by multiplying the growth capacity of each compartment with the growth limitation factor determined by the above equation, i.e.

$$\text{Actual } M_a \text{ growth rate} \quad \mu_a = \mu_a^{cap} \cdot f(c, n) \quad (17)$$

$$\text{Actual } M_b \text{ growth rate} \quad \mu_b = \mu_b^{cap} \cdot f(c, n) \quad (18)$$

The actual growth rates of above- and belowground biomass play an important role in the dynamics of all basic plant variables used in the model, as can be read from Equations 3 to 7.

LOSS OF BIOMASS

In the simulation model, functional biomass (leaves and fine roots) is lost in daily shedding processes, i.e. biomass is lost from the plant at a constant shedding rate expressed in gram shed biomass per gram existing biomass per day. Supportive biomass (stems and coarse roots) is not lost in shedding processes but remains on the plant during the full simulation period unless the plant dies during the simulation. The advantage of modeling the loss of biomass this way is that no information on the age of the biomass has to be kept, which simplifies the model considerably. However, the daily shedding fraction is difficult to measure and loss of biomass is commonly expressed in terms of longevity. The conversion of leaf longevity to biomass loss rate, described in Appendix I, is based on a standard exponential decay model (Yodzis, 1989) and results in:

$$LL - \tau \text{ relation} \quad \tau = \frac{\ln(k)}{LL} \quad (19)$$

with τ the biomass loss rate in gram shed biomass per gram existing biomass per day, LL: the longevity in days and k a constant.

In the model, leaf longevity LL is assumed to be a function of the Specific Leaf Area SLA. The underlying explanation for this relation is that leaves with a lower SLA are thicker and tougher, and thus protected against wear and tear, and also have a higher production of defensive compounds which deters herbivory (Reich *et al.*, 1998; Westoby *et al.*, 2000, 2002), thus

$$LL - SLA \text{ relation} \quad \log(LL) = a_L - b_L \cdot \log(SLA) \quad (20)$$

Consequently, the loss rate of leaf biomass can also be described as a function of SLA (Appendix I)

$$\text{Leaf loss rate} \quad \tau_a = \ln(k) \cdot e^{-a_L} \cdot SLA^{b_L} \quad (21)$$

The calculation of the loss rate of fine root biomass is analogous to that of the loss rate of leaf biomass described above. Obviously, then the root longevity (RL) and Specific Root Area (SRA) are used.

HEIGHT GROWTH AND DIFFERENTIATION BETWEEN FUNCTIONAL & SUPPORTIVE BIOMASS

As explained before, newly produced biomass is allocated to either the aboveground or the belowground plant biomass. However, biomass allocated to the aboveground compartment cannot be used fully to produce carbon-acquiring leaves. Part of the newly produced biomass has to be invested in supportive stem biomass. Similarly, belowground biomass production is divided between N-capturing fine roots and supporting coarse roots. For the description of the division of newly produced biomass between functional and supportive biomass it is more convenient to use the absolute biomass production rates in gram per day.

$$\text{Division } M_a \text{ prod. rate} \quad P_{Ma} = P_{MaL} + P_{MaS} \quad (22)$$

and:

$$\text{Division } M_b \text{ prod. rate} \quad P_{Mb} = P_{MbF} + P_{MbC} \quad (23)$$

where P_{Ma} , P_{MaL} and P_{MaS} are the absolute production rates of total aboveground biomass, functional leaf biomass and supportive stem biomass respectively, and, similarly, P_{Mb} , P_{MbF} and P_{MbC} the absolute production rates of total belowground biomass, functional fine root biomass and supportive coarse root biomass.

New leaves are placed at a constant density at the top of the aboveground cylinder. Similarly, new roots are placed at a constant density at the bottom of the belowground cylinder. Consequently, the production of functional biomass will bring about an increase in the height of the plant. Thus, the production rate of leaf biomass can be expressed as a function of the height growth and the density of leaf mass in the cylinder. Below, the set of equations used to determine the partitioning of biomass production is given for the aboveground compartment. The set of equations for the belowground compartment are similar to the set for the aboveground compartment.

$$\text{Abs. prod. rate of } M_{aL} \quad P_{MaL} = \pi \cdot r_{ac}^2 \cdot \rho_{MaL} \cdot \frac{dH_{ac}}{dt} \quad (24)$$

with r_{ac} the radius of the aboveground cylinder in meter and ρ_{MaL} the density of leaf mass in the cylinder in gram leaf per m^3 cylinder volume. Because r_{ac} and ρ_{MaL} are constant, the production rate of leaf mass depends on the height growth rate of the plant dH_{ac}/dt .

The investment in supportive biomass per meter height is not constant but changes with height of the plant. Consequently, the height of the plant can be expressed as a function of the supportive biomass.

$$H_{ac} - M_{aS} \text{ relation I} \quad H_{ac} = f(M_{aS}) \quad (25)$$

with H_{ac} the height of the plant in meters and $f(M_{aS})$ a yet to be specified function relating height and stem mass.

The height growth rate of the plant can then be calculated as:

$$\text{Height growth} \quad \frac{dH_{ac}}{dt} = \frac{df(M_{aS})}{dM_{aS}} \cdot \frac{dM_{aS}}{dt} \quad (26)$$

The explicit expression of the factor $df(M_{aS})/dM_{aS}$ will be dealt with in more detail in Equation 32.

Because, as is mentioned before, stem mass is not subject to shedding, the rate of change of stem mass dM_{aS}/dt is equal to the production rate of stem mass:

$$\text{Change in } M_{aS} \quad \frac{dM_{aS}}{dt} = P_{MaS} \quad (27)$$

Using Equation 25 the absolute production rate of stem mass may be written as:

$$\text{Abs. prod. rate of } M_{aS} \quad P_{MaS} = \left(\frac{dH_{ac}}{dt} \right) / \left(\frac{df(M_{aS})}{dM_{aS}} \right) \quad (28)$$

Now, both right-hand side terms of Equation 21, the absolute production rates of leaf and stem mass, are defined and substitution of those equations (24 and 28) into Equation 21 gives:

$$\begin{aligned} \text{Abs. prod. rate of } M_a \quad P_{Ma} &= \pi \cdot r_{ac}^2 \cdot \rho_{MaL} \cdot \frac{dH_{ac}}{dt} + \frac{1}{\left(\frac{dH_{ac}}{dM_{aS}} \right)} \cdot \frac{dH_{ac}}{dt} \\ &= \left(\pi \cdot r_{ac}^2 \cdot \rho_{MaL} + \frac{dM_{aS}}{dH_{ac}} \right) \cdot \frac{dH_{ac}}{dt} \end{aligned} \quad (29)$$

Finally, the height growth of the plant dH_{ac}/dt can be calculated as:

$$\text{Change in height} \quad \frac{dH_{ac}}{dt} = \frac{P_{Ma}}{\pi \cdot r_{ac}^2 \cdot \rho_{MaL} + \frac{dM_{aS}}{dH_{ac}}} \quad (30)$$

In order to solve the last term in the above equation that is not yet defined, $df(M_{aS})/dM_{aS}$, first the height-stem mass relation has to be described explicitly. The height-stem mass

Model description

relation used in this model is based on Greenhill's formula of the critical buckling height (Niklas, 1995), which describes the biomechanical constraints of height growth and results in an increasing stem diameter with increasing height. In Appendix II the conversion of Greenhill's formula to the height-stem mass relation used in this model is described. For the height of the aboveground cylinder, the following relation results:

$$H_{ac} - M_{aS} \text{ relation II} \quad H_{ac} = f(M_{aS}) = k_H \cdot M_{aS}^{\left(\frac{\beta}{\beta+2}\right)} \quad (31)$$

where k_H and β are parameters to shape the height-stem mass relation. Belowground a similar equation relates cylinder height H_{bc} to the coarse root biomass M_{bC} . The derivative of the above equation can then be used to solve dH_{ac}/dt and P_{MaS} as follows:

$$\text{Derivative } H_{ac}/M_{aS} \quad \frac{dH_{ac}}{dM_{aS}} = \frac{df(M_{aS})}{dM_{aS}} = k \cdot \frac{\beta}{\beta + 2} \cdot M_{aS}^{\left(\frac{\beta}{\beta+2}-1\right)} \quad (32)$$

With this set of equations the partitioning of newly produced total above or belowground biomass between functional and supporting biomass can be calculated in combination with the height growth rate of the plant.

LIGHT EXTINCTION WITHIN THE PLANT CANOPY

The model uses a simplified light climate in which light falls vertically on top of the cylinder. Diagonal light beams and diffuse light have not been taken into account. The light availability, imposed on the plant by its environment, can be either constant or seasonally varying. A seasonally variable light climate is described in the section on the light regime.

The light attenuation in the plant canopy is calculated with Beer's law (Johnson & Thornley, 1984; Monsi & Saeki, 1953),

$$\text{Light intensity} \quad i(h) = i_0 \cdot e^{-a_L \cdot \cos \alpha_L \cdot F} \quad (33)$$

where $i(h)$ is the light intensity at height h and i_0 is the light intensity directly above the plant cylinder, both in $\mu\text{mol photons per m}^2$ per second, a_L is the absorption coefficient of the leaves, α_L is the inclination of the leaves in relation to the horizontal plane in radians and F is the total leaf area in m^2 .

This light intensity is then used to calculate the interception of light by the leaves at height h , i.e.

$$\text{Light interception} \quad i_{al}(h) = a_L \cdot i(h) \cdot \cos \alpha \quad (34)$$

The aboveground cylinder of the plant is divided into layers of 5 mm height. To realistically simulate the smooth light attenuation and interception over the height of the layers in the canopy the Gaussian integration method (Press *et al.*, 1986) is used.

PHOTOSYNTHETIC CARBON GAIN

The leaf photosynthetic rate is calculated by a standard non-rectangular hyperbola that describes the relationship between the photosynthetic capacity, light interception and quantum yield (Johnson & Thornley, 1984; Marshal & Biscoe, 1980).

$$\text{Leaf photosynth. rate} \quad P_{gL}(h) = \frac{(P_{gmL} + \Phi \cdot i_{al}) - \sqrt{(P_{gmL} + \Phi \cdot i_{al})^2 - 4\theta \cdot \Phi \cdot i_{al} \cdot P_{gmL}}}{2\theta} \quad (35)$$

Leaf photosynthetic rate P_{gL} and the photosynthetic capacity P_{gmL} are expressed in $\mu\text{mol CO}_2$ per m^2 leaf per second and Φ , the quantum yield per unit absorbed light, is expressed in $\mu\text{mol CO}_2$ per $\mu\text{mol photons}$. The curvature factor θ is dimensionless. To keep the calculations of the photosynthesis simple P_{gmL} has been kept constant over the height of the cylinder, as are quantum yield and the curvature factor.

As described in the previous section, the aboveground cylinder of the plant is divided into layers of 5 mm height. The photosynthetic rate per layer is calculated by integrating Equation 35 over the height of the layer, using the Gaussian integration method (Press *et al.*, 1986), and multiplying the result with the leaf area in that layer.

$$\text{Gross phot. rate layer} \quad P_g(l) = \int_0^{H_l} dh \cdot P_{gL}(h) \cdot F(l) \quad (36)$$

with $P_g(l)$ the gross photosynthetic carbon gain rate of the layer in gram C per day and $F(l)$ the total leaf area in the layer in m^2 .

The total plant photosynthetic rate, indicated by P_g and expressed in gram C per day, then results from the addition of the gross photosynthetic rate in all layers.

In the description of the dynamics of the carbon concentration (Equation 6), the photosynthetic rate p_g is expressed in gram C per gram aboveground biomass per day.

$$\text{Relative } P_g \quad p_g = \frac{P_g}{M_{al}} \quad (37)$$

Model description

By using the above equation the photosynthetic rate P_g in gram per day can easily be converted to photosynthetic rate per gram aboveground biomass, p_g .

To prevent the C concentration in the substrate pool from getting out of control, especially in relation to the N concentration in the pool, a feedback mechanism on the photosynthetic capacity is included in the model. This mechanism reduces the photosynthetic capacity if carbon in the substrate pool is in high supply as compared to nitrogen, thus if the n/c ratio is low. If both the C and N concentrations are high, as well as when the carbon concentration is low independent of N the concentration, the photosynthetic capacity is not reduced. The feedback on the capacity P_{gmL} is given by:

$$\text{Feedback on } P_{gmL} \quad F_p = 1 - \left(\frac{c^p}{\left(\frac{n}{c} \cdot k_c\right)^p + n^p} \cdot \left(1 - \frac{n^p}{\left(\frac{c}{n} \cdot k_n\right)^p + n^p} \right) \right) \quad (38)$$

F_p is the factor with which P_{gmL} is multiplied, which lies between 1 and 0, and p determines the slope of the transition from $F_p = 1$ to $F_p = 0$. The parameters k_c and k_n determine the range of n/c ratios where F_p changes from 1 to 0. In Figure 4 the course of the feedback factor is visualized as a function of the C and N concentrations.

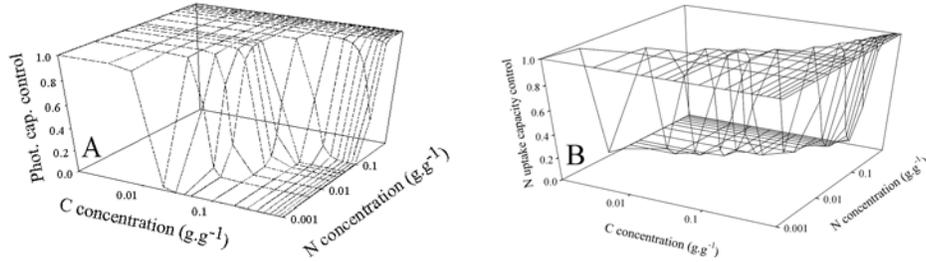


Figure 4 Visualization of the feedback mechanism on photosynthetic capacity (A) and nitrogen uptake capacity (B). If the control factor, shown on the z-axis, equals one, the capacity is not reduced, if it equals 0 the capacity is reduced completely.

N AVAILABILITY IN THE SOIL AND NITROGEN UPTAKE

The soil compartment in the model is divided into three sections (Figure 5). The ambient soil represents the habitat conditions the plant is growing in. The nitrogen concentration in this soil section is assumed to be constant and cannot be affected by the plant. The adjoining soil section, the rooting cylinder, is surrounded by the ambient soil. The nitrogen concentration in the rooting cylinder is assumed to be constant in space but can

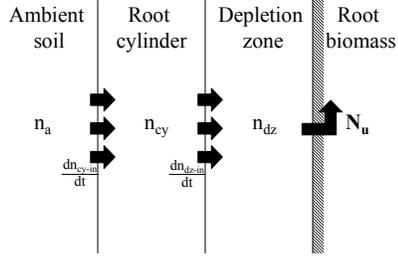


Figure 5 Schematic representation of the soil compartment and the processes involved in nitrogen transport and uptake. The arrows represent diffusion from one soil compartment to another and the uptake of nitrogen N_u ; n_a , n_{cy} and n_{dz} represent the nitrogen concentrations in the ambient soil, the root cylinder and the depletion zone respectively.

differ in time. Via this section nitrogen moves from the ambient soil to the depletion zone, an infinitely thin layer in between the fine roots and the rooting cylinder. Transport is assumed to be one-directional and only along the shortest direct trajectory from ambient soil to root. Nitrogen is taken up from the depletion zone into the part of the plant cylinder that represents the root.

The nitrogen concentrations in the rooting cylinder and the depletion zone are determined by the inflow and outflow of nitrogen from these sections. Because an equilibrium is assumed between the in and

outflow from each layer, at any time t the concentrations in the rooting cylinder and depletion zone can be derived from:

$$\text{Balance } N \text{ fluxes} \quad F_{cy}^{in} = F_{cy}^{out} \quad (39)$$

$$\text{and} \quad F_{dz}^{in} = F_{dz}^{out} \quad (40)$$

where F_{cy}^{in} is the flux into the rooting cylinder, F_{cy}^{out} the flux out of the rooting cylinder, F_{dz}^{in} the flux into the depletion zone and F_{dz}^{out} the flux out of the rooting cylinder, all in gram N per day. Since the nitrogen flowing out of the rooting cylinder enters the depletion zone, F_{cy}^{out} equals F_{dz}^{in} . The nitrogen leaving the depletion zone F_{dz}^{out} represents the uptake by the roots, so $F_{dz}^{out} = N_u$, the uptake rate of nitrogen by the root biomass.

The inflow rate of nitrogen in the rooting cylinder F_{cy}^{in} is the result of diffusion from the ambient soil, i.e.

$$\text{Influx rooting cylinder} \quad F_{cy}^{in} = 2\pi \cdot r_{bc} \cdot H_{bc} \cdot \frac{(n_a - n_{cy})}{R_{nc}} \quad (41)$$

with r_{bc} and H_{bc} the radius and height of the rooting cylinder respectively, both in meter, n_a and n_{cy} the nitrogen concentrations in the ambient soil and in the rooting cylinder in gram N per m^3 soil and R_{nc} the resistance for nitrogen transport from the ambient soil to the rooting cylinder in days per meter.

The outflow rate of nitrogen from the rooting cylinder, also resulting from diffusion, equals the inflow rate to the depletion zone:

Model description

$$\text{Influx depletion zone} \quad F_{dz}^{in} = M_{bF} \cdot SRA \cdot \frac{(n_{cy} - n_{dz})}{R_{nd}} \quad (42)$$

Because the depletion zone is defined as an infinitely thin layer surrounding the fine roots, the area over which diffusion takes place equals the total fine root area, $M_{bF} \cdot SRA$, with M_{bF} in gram and Specific Root Area SRA in m^2 per gram. R_{nd} is the resistance for nitrogen transport from the rooting cylinder to the depletion zone and n_{dz} is the nitrogen concentration in the depletion zone in gram N per m^3 soil.

The uptake rate of nitrogen by the fine root biomass of the plant determines the flux out of the depletion zone. The uptake rate of nitrogen N_u in gram per day is modeled as a Michaelis-Menten equation. If the nitrogen concentration in the depletion zone n_{dz} is high, the nitrogen uptake capacity N_u^{cap} is reached, if n_{dz} is low, the uptake rate is slowed down:

$$\text{Nitrogen uptake rate} \quad N_u = M_{bF} \cdot SRA \cdot N_u^{cap} \cdot \frac{n_{dz}}{k_{nd} + n_{dz}} \quad (43)$$

where N_u^{cap} is expressed in gram per day and k_{nd} is the semi-saturation constant for nitrogen uptake capacity.

In the description of the dynamics of the nitrogen concentration in the substrate pool (Equation 7) N uptake n_u was expressed in gram N per gram belowground biomass per day,

$$\text{Relative } N_u \quad n_u = \frac{N_u}{M_{bF}} \quad (44)$$

By using the above equation the N uptake rate N_u in gram per day can easily be converted to the uptake rate per gram belowground biomass, n_u .

To prevent the N concentration in the substrate pool from getting out of hand in relation to the C concentration in the pool, a similar feedback mechanism on the nitrogen uptake capacity as on the photosynthetic capacity is included in the model. This mechanism reduces the nitrogen uptake capacity if nitrogen in the substrate pool is in high supply as compared to carbon.

$$\text{Feedback on } N_u^{cap} \quad F_{nu} = 1 - \left(\frac{n^{p_n}}{\left(\frac{c}{n} \cdot k_n\right)^{p_n} + c^{p_n}} \cdot \left(1 - \frac{c^{p_n}}{\left(\frac{n}{c} \cdot k_c\right)^{p_n} + c^{p_n}} \right) \right) \quad (45)$$

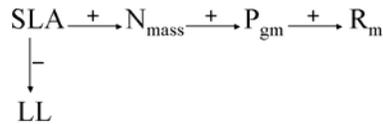
where F_{nu} is the factor with which N_u^{cap} is multiplied (that lies between 1 and 0) and p_n shapes the slope of the transition from $F_{nu} = 1$ to $F_{nu} = 0$. The parameters k_c and k_n

determine the range of n/c ratios where F_{nu} changes from 1 to 0. The course of this feedback factor is also visualized in Figure 4.

MODEL SPECIES DEFINITION

In the model different species can be defined. Species can vary in a set of leaf functional and root functional traits, as well as in level of plasticity.

As described in the introduction, traits within the sets of functional traits are not independent but are correlated based on morphological and physiological constraints, in the following way:



All relations are described as bi-variate linear relations to keep their role in the model comprehensible. In Table II the correlated trait relations used in the species definition are given, together with the literature sources they are based on. In Figure 6 the graphic representation of the relations is given. This leads to the definition of a species range spanning from species with low SLA, low leaf N_{mass} , low photosynthetic capacity and low maintenance respiration but high leaf lifespan to species with high SLA, high leaf N_{mass} , high photosynthetic capacity and high maintenance respiration but low leaf lifespan. The set of root functional traits used for the species definition is analogous to the set of leaf functional traits: Specific Root Area, root N_{mass} , nitrogen uptake capacity, root maintenance respiration and root lifespan. The correlation scheme is equivalent for both above and belowground sets and these are not independent. A high SLA always corresponds with a high SRA and correlated traits, and a low SLA is connected to low SRA values.

Table II Correlated trait relations, parameters settings and literature sources.

Relation	
1	$\log(\text{LL}) = -2.16 - 2.326 * \log(\text{SLA})$
2	$N_{\text{si}} = 0.02025 + 0.77 * \text{SLA}$
2	$P_{\text{gm}} = -0.0115 + 9.23 * N_{\text{si}}$
3	$R_m = -0.023 + 0.12 * P_{\text{gm}}$

1 Reich *et al.* (1992)
 2 Reich *et al.* (1998a)
 3 Reich *et al.* (1998b)

The level of plasticity in biomass allocation of the model plant can be set by the parameters of Equation 13. By setting $\text{Max} = 1$ a completely rigid species is obtained. Further effects of parameter values on the level of plasticity are illustrated in the result section of this chapter.

Model description

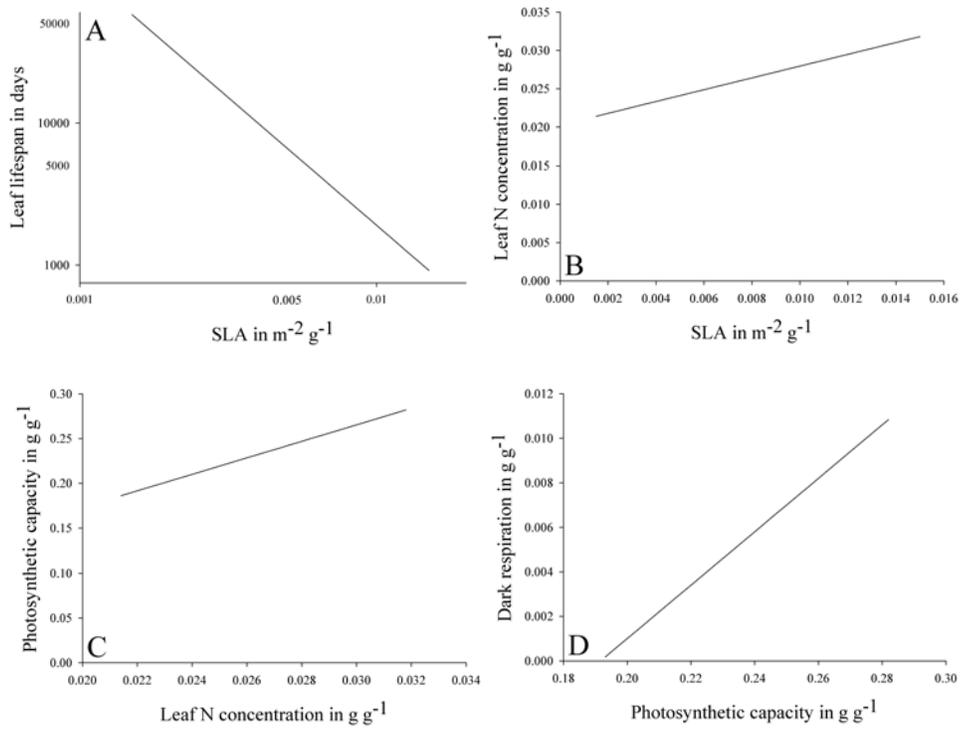


Figure 6 Correlated trait relations used in the species definition. A) SLA – Leaf Lifespan relation; B) SLA – Leaf nitrogen concentration relation; C) Leaf nitrogen concentration – Photosynthetic capacity relation; D) Photosynthetic capacity – Dark respiration relation. Correlations are based on literature data as is presented in Table II.

All other parameters were taken as constants for all species. The values are listed in Table III. If possible, parameters were taken directly from indicated literature sources. In a few cases it was not possible to obtain values directly from the literature, and the specific parameter had to be estimated.

LIGHT REGIME

In deciduous forest systems the light availability changes predictably over the growing season. To mimic the development of light availability over the growing season in deciduous forest systems a reverse generalized logistic or Richard's curve is used (Figure 7):

$$\text{Forest interception} \quad i_0 = A + \frac{C}{\left(1 + \left(T \cdot e^{-B(t-M)}\right)^{1/T}\right)} \quad (46)$$

in which i_0 is the light availability above the forest understory layer, t is the time in days, A and C are parameters to control respectively the lower and upper asymptotes of the curve, T is a parameter to control where the strongest decrease in light availability occurs, nearer to the lower or upper asymptote, B is a parameter to control the rate of the strongest decrease and M a parameter to control the time at which the maximum decrease occurs. The growing season starts in the beginning of april, $t=0$, and lasts until the end of August at $t=150$. The forest canopy interception i_0 is calculated as a percentage of the light availability above the forest canopy. The percentage light availability at the forest floor thus results from $100-i_0$. In the photosynthesis calculations of the model, the light availability is expressed in $\mu\text{mol photons per m}^2$ per second. The light availability above the forest canopy is assumed to be constant at $1200 \mu\text{mol per m}^2$ per second during the full course of the simulation. Consequently, the light availability in $\mu\text{mol per m}^2$ per second is defined as $(100-i_0)*1200$.

RESULTS

GENERAL INFORMATION

The model plant is a simplification of a real plant, designed to study the role of Specific Leaf Area and shoot-to-plant ratio on the performance of plants grown in different environments. Still, the behavior of the model plant should satisfy certain conditions. Since the performance of the plant is measured from total plant mass, the model plant should show a realistic biomass production that is affected by the plant traits of interest (SLA and shoot-to-plant ratio). Observed patterns should be explainable and simplifications should not affect the qualitative behavior of the plant. The simulations below show the implications of assumptions and simplifications used on the growth of the model plant. Furthermore, the simulations illustrate how processes involved in the resource economy, i.e. photosynthesis, maintenance respiration and investment in

Table III List of standard parameter settings and literature sources.

Abbreviation	Value	Unit
r_{nu}	*	$0.00125 \text{ g g}^{-1} \text{ d}^{-1}$
c_c	*	0.8 g g^{-1}
n_r	¹	0.014 g g^{-1}
k_c	*	0.2
k_n	*	0.05
c_{min}	*	0.05 g g^{-1}
n_{min}	*	0.01 g g^{-1}
c_{leth}	*	0.001 g g^{-1}
n_{leth}	*	0.001 g g^{-1}
k	*	0.02
r_{ac}, r_{bc}	*	0.075 m
ρ_{MaL}, ρ_{MBr}	*	3000 g m^{-3}
k_H	*	0.25
β	*	1.279
a_L	²	0.82
α_L	³	20 rad
Φ	⁴	$0.05 \text{ } \mu\text{mol } \mu\text{mol}^{-1}$
θ	⁴	0.8
R_{nc}, R_{nd}	*	0.1 d m^{-1}
k_{nd}	*	0.0714
p	*	1
p_n	*	5

* estimated
** mathematical parameter
¹ Aerts (1996)
² Rosati et al. (2001)
³ Schieving (1998)
⁴ Anten (1995)

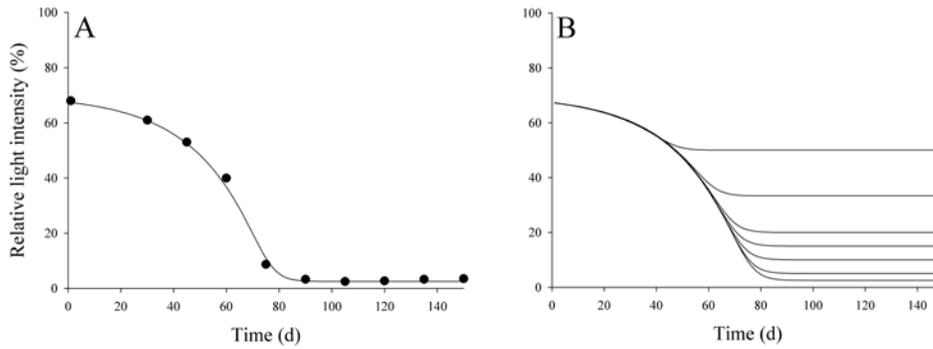


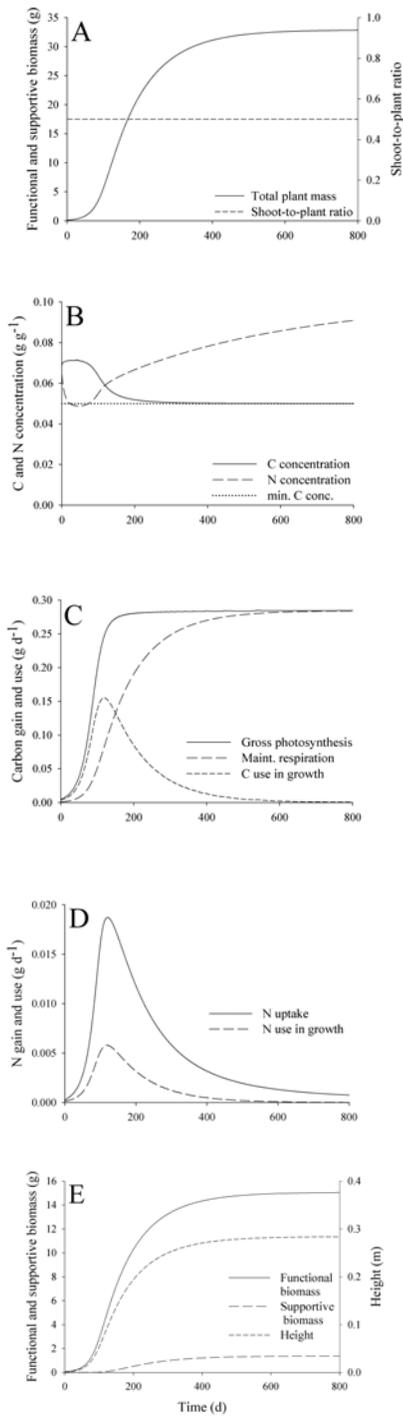
Figure 7 A) Course of the light availability on the forest floor described by a Richard's curve fitted to data of Pons (1977). B) Different light regimes can be mimicked, all starting at the same light availability but decreasing to different levels in the second part of the simulation period.

growth, change in the course of time and affect the behavior of the model plant. This will allow a better understanding of the simulations presented in other chapters.

First the behavior of a rigid plant species, not capable of adjusting its shoot-to-plant ratio, is described. The consequences of biomass loss and height growth, the feedback mechanism on the C and N uptake capacity, resource availability and leaf functional traits on plant performance are explained. Secondly, the behavior of a plant that is plastic in its biomass allocation is demonstrated. Besides the effect of model plant features on plant performance, the allocation mechanism and the role of its parameters is studied in more detail.

RIGID PLANT SPECIES WITHOUT BIOMASS LOSS

To evaluate the behavior of a rigid model plant, first a simulation was run of a model plant that never sheds its leaves and fine roots ($\tau_a = \tau_b = 0$). Values of the other parameters are shown in Table III. For this plant initially a fast increase in biomass is expected that slows down as maintenance respiration, due to the increase of biomass in combination with increasing self-shading, draws level with gross photosynthesis. Eventually, maintenance respiration is expected to equal gross photosynthesis and growth is expected to stop completely resulting in a constant biomass. As is illustrated in Figure 8A (total plant mass) and Figure 8C (C gain and use) the plant followed the expected path and reached this state of constant biomass after approximately 800 days. Since the plant was not plastic in its biomass allocation, shoot-to-plant ratio remained constant at the initial level. The partitioning of biomass into functional (leaves and fine roots) and supportive (stems and coarse roots) biomass as well as the development of height, both shown in Figure 8E for the aboveground biomass, was similar for the above and belowground plant.



Analogous to the development of the total plant mass, all variables shown in this figure initially increased rapidly but leveled off as growth stopped.

Growth of the model plant is driven by the C and N concentrations in the substrate pool. These concentrations, in turn, are set by a combination of inflow of C and N from photosynthesis and N uptake, outflow of C and N to support growth and of C to maintenance respiration and the container size of the substrate pool, represented by the total plant biomass. As is shown in Figure 8B, initially both carbon and nitrogen in the substrate pool are in ample supply, enabling the fast growth in the beginning of the simulation. Then, a strong decrease in the carbon concentration followed. In this phase plant growth was fast, photosynthetic rate increased rapidly but the costs of growth and maintenance became higher. Furthermore, the increase in total plant mass caused a severe dilution of the C concentration. These processes resulted in a decrease of the C concentration in the substrate pool and slowed down the biomass production until the plant reached the constant total plant mass. As maintenance respiration became equal to gross photosynthesis the C concentration went down to the minimum level (indicated by the dotted horizontal line), growth stopped and the plant reached its final biomass. The N concentration in the substrate pool showed the opposite response but did not level off at the end of the simulation. Already from the beginning, in spite of the increased N demand to support the fast growth and the dilution effect due

Figure 8 Development in time of a rigid model plant species that never sheds its leaves simulated at $i_{h_0} = 800 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $n_a = 0.1$. A) total plant mass and shoot-to-plant ratio; B) carbon and nitrogen concentrations in the substrate pool and the minimum C concentration for growth; C) gross photosynthetic rate, rate of carbon demand for maintenance respiration and carbon use in growth; D) rate of nitrogen uptake and nitrogen use in growth; E) functional and supportive biomass of both the above and belowground plant and height of the above and belowground plant.

Results

to increase of the pool container, the N uptake exceeded N use (Figure 8D) to such extent that the N concentration increased. However, this increasing N concentration did not affect growth positively because the C concentration started limiting growth. As the carbon concentration decreased further and growth slowed down strongly, N demand decreased further. The N concentration in the substrate pool did not continue to increase endlessly. Due to the feedback mechanism on N uptake at high N concentrations in the substrate pool, as described in the model description, nitrogen uptake decreased and caused the strong increase in N concentration to gradually slow down.

As is shown in Figure 9A, the effect of this feedback on N uptake on the total biomass production of the plant is only small. The plants lacking the feedback mechanism grew slightly faster than the plants with the feedback. This can be attributed to the high N availability to support fast growth in the plants lacking the feedback mechanism. A larger effect was found on the N concentration in the substrate pool (Figure 9B to E). The N concentration of plants lacking the feedback started increasing from the beginning of the simulation and did not level off.

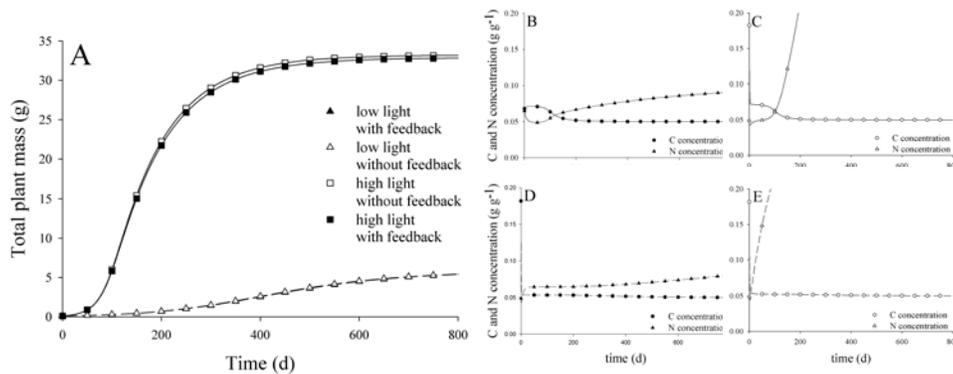


Figure 9 The effect of a feedback mechanism on N and C acquisition on A) total biomass production of a plant with and without the feedback at high concentrations in the substrate pool for plants grown at a light availability (i_{h0}) of 1200 (high) and 150 (low) $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and C and N concentrations of a plant B) with the feedback simulated at $i_{h0} = 800 \mu\text{mol m}^{-2} \text{s}^{-1}$, C) without the feedback simulated at $i_{h0} = 800 \mu\text{mol m}^{-2} \text{s}^{-1}$, D) with the feedback simulated at $i_{h0} = 150 \mu\text{mol m}^{-2} \text{s}^{-1}$ and E) without the feedback simulated at $i_{h0} = 150 \mu\text{mol m}^{-2} \text{s}^{-1}$.

From the above simulation it can be concluded that if the model plant cannot lose biomass, the plant develops in approximately 800 days to a balanced state in which growth has stopped and net photosynthetic rate has gone to zero as a result of self-shading and respiration. The above simulations of the non-shedding plant contribute to the understanding of the growth processes of the model plant. However, it is more realistic to include shedding of biomass. Such a version of the model is used in the simulations of the rigid plant below.

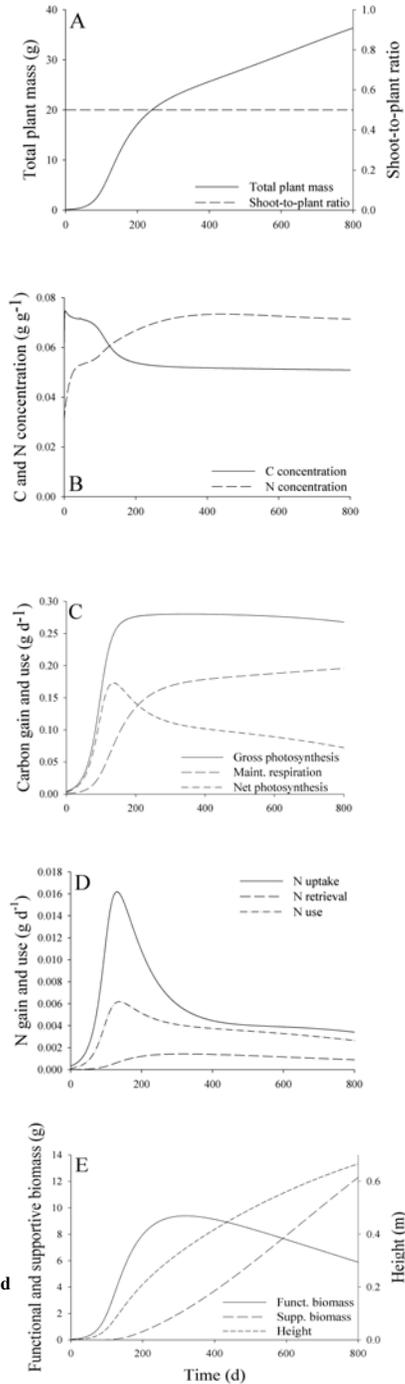
RIGID PLANT SPECIES WITH BIOMASS LOSS

When shedding of leaves and fine roots was introduced the picture changed. Firstly, in the initial phase of rapid growth the biomass increase of the shedding plant was slower than that of the plant that never sheds its biomass. Secondly, after the initial phase of fast growth the increase of biomass slowed down but total plant biomass did not level off to a constant level (Figure 10A) as in the earlier simulation (Figure 8A).

The slower increase in biomass in the phase of rapid growth was due to the negative effect of the loss of biomass on net biomass accumulation. The continuation of growth at the end of the simulation was the indirect result of the loss of biomass. In the non-shedding plant, growth stopped as the result of two processes: 1) self-shading reduced gross photosynthesis and, 2) maintenance respiration costs increased with increasing biomass. In the shedding plant, severe self-shading is prevented since leaf mass is lost from the plant. Furthermore, because new leaves are placed at the top of the plant, production of new leaf mass requires production of supportive stem mass. Since supportive stem mass is cheaper to maintain than leaf mass, maintenance respiration demands did not increase as fast as in the non-shedding plant (Figure 10C). Consequently, the net photosynthesis remained positive, the C concentration in the substrate pool did not go down to the minimum level at the end of the simulation and the plant kept growing (Figure 10B).

The nitrogen concentration in the substrate pool also showed a different pattern with shedding as compared to the simulation without shedding

Figure 10 Development in time of A) total plant mass and shoot-to-plant ratio; B) carbon and nitrogen concentration in the substrate pool; C) photosynthetic carbon gain, carbon used for maintenance respiration and carbon used in growth; D) nitrogen uptake rate, nitrogen retrieval from shed biomass and nitrogen used in growth; E) height and partitioning between functional and supportive biomass, for a standard rigid model plant.



(Figure 10B). Initially, the nitrogen concentration followed the same path but after approximately 180 days, the N concentration of the shedding plant bended off. Figure 10B and D show that, due to the high nitrogen concentration in the pool, N uptake is strongly reduced, while N use in growth processes, in contrast to the simulation without shedding, remained at a relatively high level. The expansion of the container size of the substrate pool, represented by total plant mass, causes the N concentration to decrease. Reallocation from shed biomass did not contribute strongly to the inflow to the substrate pool, especially in the beginning of the simulation period.

In the long run this plant is self-destructive (data not shown). Since functional biomass decreased (Figure 10E) and continued to decrease in simulations run over longer time spans, photosynthetic carbon gain went down and ultimately the plant was not able to cover its maintenance costs and died. Obviously, though it served a function in explaining the general behavior of the model plant, a growing season does not last 500 days. The standard simulation periods used in this chapter are 150 days and 180 days.

In environments where resource availability is high, plants are expected to grow fast and produce a large amount of biomass; in poor resource environments, growth generally is slow and biomass production low. This pattern is also found in the biomass production of the model plant (Figure 11). If either one of the resources is in low supply, growth is also slow and the total biomass production in 150 days is low. An interactive effect of growing conditions was found; the higher the availability of one resource, the larger the effect of the availability of the other resource on total biomass production during the simulation.

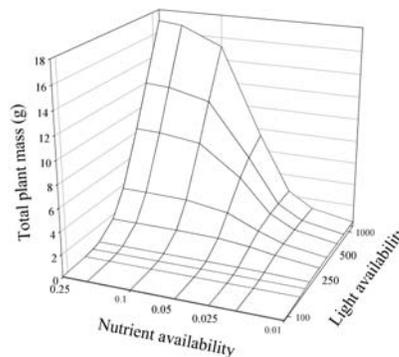


Figure 11 Effect of light and nitrogen availability on total biomass production over 150 days.

THE ROLE OF LEAF FUNCTIONAL TRAITS

The role of Specific Leaf Area (SLA) and correlated traits (N_{mass} , R_m , A_{mass} and leaf lifespan) in the development of the plant over time is illustrated in Figure 12. In the beginning of the simulations plants with a higher SLA increased in biomass faster. In this phase, plants possessing a high SLA had a large photosynthetic area with a high photosynthetic capacity (A_{mass}) and could thus acquire and spend carbon faster than the species with a lower SLA. At the end of the simulation the pattern turned. As total plant mass increased, self-shading and maintenance respiration started to play a more important role in the plants carbon budget and, since a high SLA is correlated with high

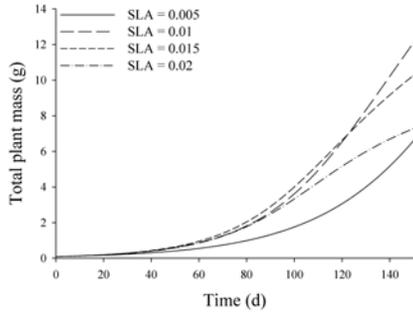


Figure 12 Effect of SLA and correlated traits on the development of total plant mass in time.

maintenance costs, this effect was more severe for the high-SLA species. Also, with increasing biomass, the effect of self-shading on gross photosynthesis increased and, due to the larger leaf area of high-SLA species, this negative effect on the carbon budget was also stronger for the high-SLA species. After 150 days, the plant with the one-but-highest SLA reached the highest biomass. As can be concluded from Figure 12, the ranking in biomass production of species with different SLA-values is strongly dependent on the point of time at which the evaluation takes place. The shorter the time-

interval over which the evaluation takes place, the higher the SLA-value at which the highest biomass is reached. Would the evaluation-interval be increased, the plant with the lowest SLA would achieve the highest total biomass.

VERTICAL LEAF MASS DISTRIBUTION

The aboveground model plant is built up of layers that are filled from the bottom upwards while the plant grows, placing new leaves only at the top of the plant. Shedding of biomass starts the moment the biomass is produced. Consequently, the vertical distribution of leaf biomass will not be equal. Figure 13 shows the biomass distribution of a standard plant after 150 days; the total amount of leaf mass was lowest in the bottom layer and increased with height. The largest amount of leaf mass was present in the one-but-highest layer. The highest layer had not yet reached the maximum amount of leaf mass at the end of the simulation period.

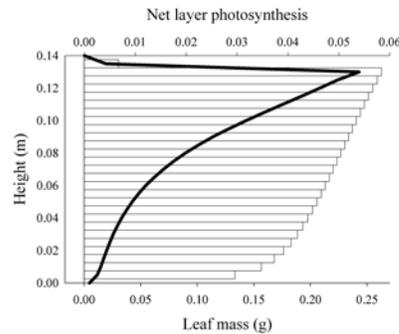


Figure 13 Vertical distribution of leaf biomass at the end of a simulation (bars) and net layer photosynthesis over height (line).

The bold line Figure 13 represents the net layer photosynthesis, so the carbon acquired by the leaves in that layer, minus the carbon used in maintenance respiration of the leaves in that layer. The net photosynthesis in the severely shaded bottom layers was close to zero. The costs for maintenance of the leaf mass that was left in these layers just balanced the gross photosynthesis of the layer at the low light conditions at this depth in the plant canopy. The carbon demands for the maintenance of the stems and the root compartment

plus the carbon investment needed for growth had to be paid for by the positive net photosynthesis of the layers higher in the canopy.

HEIGHT GROWTH

By changing the density of the functional biomass, i.e. the amount of leaf or fine root biomass per layer, the plant can change its height growth strategy. With a high density, the plant will grow in height only slowly and thus will have relatively low costs of supportive biomass. In contrast, a low density will bring about a fast growth in height with the accompanying relatively high costs for supportive biomass leaving relatively less for functional biomass. It is clear that a change in height growth strategy can entail an advantage in a competitive situation. For plants growing in isolation, the balance between investments in height growth and in functional biomass has important consequences for the total biomass production. This is clearly illustrated in Figure 14A. The plant with the lowest leaf density and the strongest investment in height produced the least biomass in 150 days. This is due to the relatively small amount of functional biomass this plant had, causing the absolute amount of carbon and nitrogen the plant acquired to be low. A high

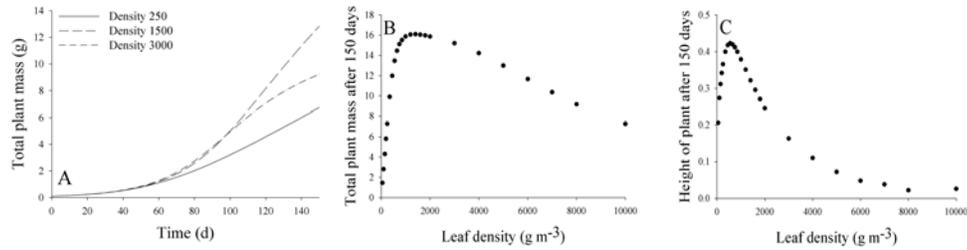


Figure 14 Total plant mass in time for plants differing in leaf density (A), solid line represents the plant with the lowest leaf density, the dash-dotted line the plant with the highest leaf density. Total plant mass (B) and height of the plant (C) as function of leaf density.

leaf density caused self-shading to occur already early in the simulation, due to the relatively high investment in functional biomass, causing growth to slow down. In this example, the plant with the intermediate density, a density of 1500 g m⁻³, reached the highest biomass. This plant possessed a sufficient amount of functional biomass to acquire carbon and nitrogen but also invested strong in height growth, thus producing a large amount of supportive biomass which contributed to the total plant biomass. For a solitary growing plant a certain optimum in density of functional mass and corresponding partitioning between supportive and functional biomass can be found at which total biomass production is highest (Figure 14B). Logically, the density at which height growth was maximal was found at a lower density (approximately 500 g m⁻³), at the point where the amount of leaf biomass was sufficient to support fast growth but where the lower density brought about a stronger investment in supportive biomass and height (Figure 14C)

PLASTIC PLANT SPECIES WITHOUT BIOMASS LOSS

As is explained in the model description, besides a rigid allocation to shoot and root, used in the simulations above, the model plant can also be set to a plastic allocation pattern.

The plastic plant is capable of steering its shoot-to-plant ratio towards the plant compartment involved in the acquisition of the most limiting resource. Which resource is most limiting growth is determined based on the n/c ratio in the substrate pool.

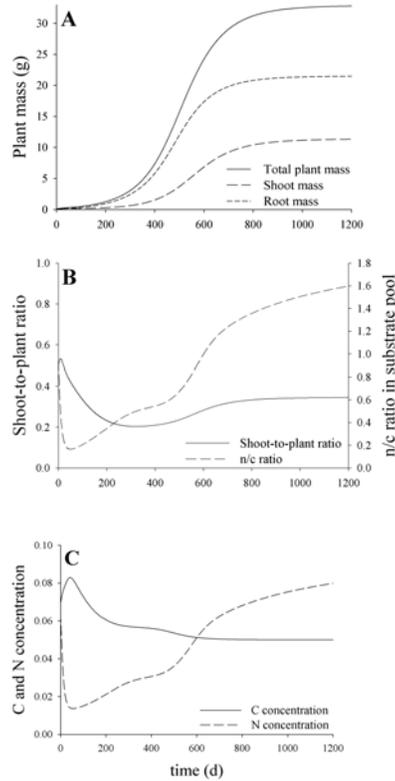


Figure 15 A) Total plant mass, shoot mass and root mass, B) Shoot-to-plant ratio and n/c ratio in the substrate pool and C) carbon and nitrogen concentration in the substrate pool of a plastic plant that never sheds its leaves and fine roots, grown at high light intensity ($i_0 = 800 \mu\text{mol m}^{-2} \text{s}^{-1}$) and a nitrogen supply (n_a) of 0.01. Plasticity parameters: $\kappa = 2$, $\text{Max} = 4$, $\alpha = 1.2$.

To evaluate the behavior of the plastic plant first a simulation was run for a model plant that never sheds its leaves and fine roots ($\tau_a = \tau_b = 0$).

Analogous to the growth of a rigid plant species, in the growth of a plastic plant species that does not lose any biomass two phases could be distinguished. Initially, when the plant was still small, a phase of fast growth occurred in which biomass increased rapidly. Ultimately, the plant reached a constant biomass; self-shading decreased gross photosynthesis and biomass production increased maintenance respiration until gross photosynthesis equaled maintenance respiration and growth stopped. This is illustrated by the solid line in Figure 15A, which represents the total plant mass as a function of time of a plastic plant growing in a high light environment ($i_0 = 800 \mu\text{mol m}^{-2} \text{s}^{-1}$) and at low nitrogen availability ($n_a = 0.01$). The transition between the two phases took place gradually and in fact covered the largest part of the simulations. In general, this pattern did not differ from the pattern found in biomass production in the rigid plant, and the underlying growth processes, based on the availability of carbon and nitrogen in the substrate pool, are also in accordance with those of the rigid plant species. The development of the shoot-to-plant ratio was different for the plastic plant (Figure 15B). As could be expected in the high-light, low-N environment, initially the shoot-to-plant ratio of the plant decreased strongly. However, later in the

simulation, the shoot-to-plant ratio increased again and then leveled off to a constant value. Formally, the proportional allocation direction of the model plant is determined by the n/c ratio in the substrate pool and the reference value of the n/c ratio v_{ref} , both represented in

Figure 15B. From Figure 2 it can be read that if the n/c ratio in the substrate pool is smaller than the reference value, the plastic plant increases the belowground growth rate at the cost of the growth of the aboveground compartment; when the value of the n/c ratio is above v_{ref} the proportional allocation is opposite. The n/c ratio, in turn, is determined by a combination of environmental conditions and the growth phase of the plant. The initial strong decrease in n/c ratio, shown in Figure 15B that leads to a decreasing shoot-to-plant ratio in the beginning of the simulation, was due to the acclimation of the plant to the environment in combination with the initial status of the plant. The nitrogen concentration decreased fast (Figure 15C), caused by the low nitrogen environment the plant was growing in, the relatively high initial shoot-to-plant ratio and the high N demand in this period of fast growth. The high shoot-to-plant ratio also caused the carbon concentration to increase. Consequently, the n/c ratio, which already started out below the reference value v_{ref} , indicated by the dotted horizontal line, fell even further below v_{ref} . As long as the n/c ratio remained below v_{ref} , the shoot-to-plant ratio kept decreasing but, due to the relative increase in root mass, and thus the increased uptake of nitrogen that exceeded the demand, the n/c ratio increased again. The moment the n/c ratio crossed the reference value the shoot-to-plant ratio started increasing as well. Although this had a positive effect on the aboveground biomass and thus on the acquisition of carbon, this did not lead to a decrease in n/c ratio. Because the growth of the plant was slowing down and the plant grew towards the final constant total plant mass, the nitrogen demands declined while the carbon demands, due to increasing maintenance costs, exceeded the carbon inflow to the pool, resulting in a continued increase in n/c ratio.

At the end of the simulation period, as growth had stopped and the total plant mass became constant, the shoot-to-plant ratio also did not change any more. This illustrates the effect of absolute resource availability in the substrate pool on the rate of change of the shoot-to-plant ratio. Besides the relative division between above and belowground growth rate, based on the relative availability of carbon and nitrogen in the substrate pool, also the absolute concentrations of carbon and nitrogen are involved. As is shown in Figure 15C, the carbon concentration reached a minimum value, indicated by the dotted horizontal line, at the end of the simulation period. According to Equation 16, if either the carbon or the nitrogen concentration reaches the minimum value, the growth limitation factor $f(c,n)$ becomes zero. As can be read from the Equations 17 and 18, if $f(c,n)$ is zero, the actual growth rate of both above and belowground biomass also becomes zero. The division of the growth capacity between aboveground growth and belowground growth capacity, calculated in the Equations 9 and 13, is then no longer relevant. If the actual growth rates are zero, the rate of change in shoot-to-plant ratio σ also becomes zero (Equation 5). Thus, a fast-growing plant can change its σ fast, a slow-growing plant can change its σ only slowly and a non-growing plant cannot change its σ at all.

The effect of the feedback mechanism on N uptake in the plastic plant was comparable to that of the rigid plant. The effect on biomass production was only small and positive for the plant lacking the feedback mechanism (Figure 16A); the effect of the feedback

mechanism on the N concentration in the substrate pool was high, preventing an excessive increase in N concentration as occurred in the plants lacking the feedback mechanism (Figure 16B to E). Although the N concentration in the substrate pool did not increase as fast as in the rigid plant, the possibility to allocate newly produced biomass towards the

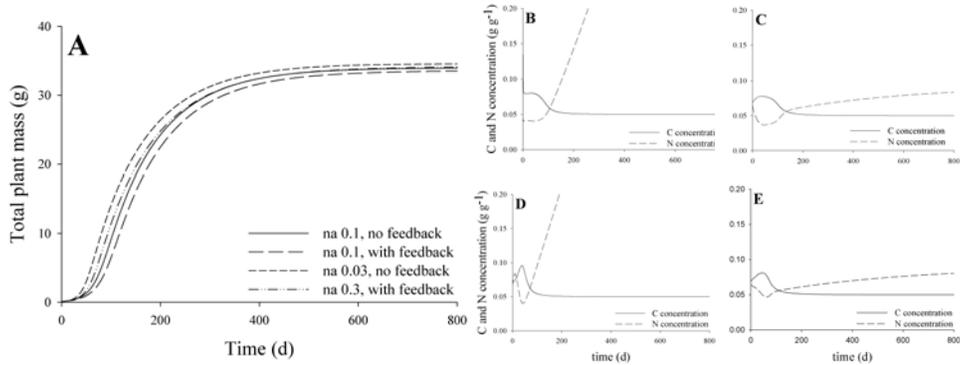


Figure 16 The effect of a feedback mechanism on N-uptake of a plastic plant on A) total biomass production of a plant with and without the feedback simulated at two different nitrogen availabilities ($n_a = 0.1$ and $n_a = 0.3$) and C and N concentrations of a plant B) without the feedback simulated at $n_a = 0.1$, C) with the feedback simulated at $n_a = 0.1$, D) without the feedback simulated at $n_a = 0.3$ and E) with the feedback simulated at $n_a = 0.3$.

aboveground compartment as nitrogen was in ample supply did not prevent the N concentration to increase shortly after the start of the simulation. Because the shoot-to-plant ratio became constant when shedding was not possible, this plant is very suitable for analyzing the effect of the environment on the shoot-to-plant ratio. The effect of the environment on this plant should not be confused with the effect of environment on an exponentially growing model plant, which is mostly used in allocation modeling studies (e.g. Hilbert & Reynolds, 1991; Reynolds & Chen, 1996; Thornley, 1998). The constant shoot-to-plant ratio found in an exponentially growing plant represents a balance between resource acquisition in photosynthesis and N uptake and the use of these resources in investment of new biomass. This results in a steady state situation in which the internal C and N concentrations, the shoot-to-plant ratio and the RGR do not change any more. Thus, the steady state situation of an exponentially growing plant is a direct reflection of the growing conditions; the plant adjusts its shoot-to-plant ratio such that the acquisition of C and N equal the investment in growth. As is explained above, initially the environment played an important role in the change in shoot-to-plant ratio. However, later in the simulation the leaves were more and more affected by self-shading and carbon was more and more used for maintenance of the existing biomass. These factors, both of which are often not included in exponential allocation models, gained in importance in the course of the simulation, with growth of the plant, and generated an increasing need for aboveground biomass. Consequently, at the end of the simulation, independent of environmental conditions, the plants started allocating stronger towards the aboveground biomass and shoot-to-plant ratio increased

(Figure 17). The rate with which the plant was capable of increasing its shoot-to-plant ratio depended on the initial change in shoot-to-plant ratio and the growth rate at the end of the simulation.

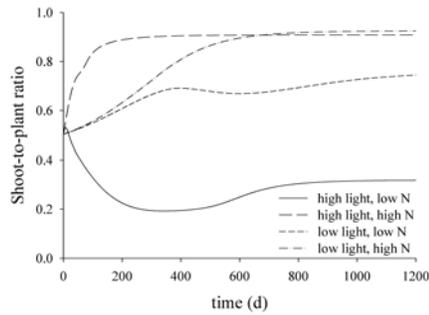


Figure 17 Shoot-to-plant ratio in time of the non-shedding plastic plant species, growing at high ($i_{h0} = 1200 \mu\text{mol m}^{-2} \text{s}^{-1}$) and low ($90 \mu\text{mol m}^{-2} \text{s}^{-1}$) light availability and high ($n_a = 0.3$) and low ($n_a = 0.01$) nitrogen availability. Plasticity parameters: $\kappa = 2$, $\text{Max} = 4$, $\alpha = 1.2$.

The constant shoot-to-plant ratio found at the end of the simulation for a range of light and nitrogen availabilities in the environment is presented in Figure 18. As expected, the higher the light availability, the lower the constant value of the shoot-to-plant ratio, so the lower the proportional investment in aboveground biomass. A clear interaction with nitrogen availability was found since this effect was much stronger at low nitrogen availability than when nitrogen was in ample supply. The nitrogen availability had a positive effect on the shoot-to-plant ratio and this effect was stronger at high light availability than at low light availability.

PLASTIC PLANT SPECIES WITH BIOMASS LOSS

As explained in the simulations about the rigid plant, if shedding of leaves and fine roots was included in the growth processes of the plant, the plant did not grow into a biomass steady state. As is shown in Figure 19A this also applied to the plastic plant. At the end of the simulation period the plant continued to increase its biomass as a surplus of carbon in the substrate pool to invest in growth was maintained. This was enabled by the partial replacement of functional biomass for supportive biomass, which is less costly to maintain.

The maintained growth at the end of the simulation had consequences for the development of the plastic shoot-to-plant ratio. If the actual plant growth rate does not go to zero, the shoot-to-plant ratio will also continue to change, provided that the n/c ratio does not equal the reference value v_{ref} . This is illustrated Figure 19B. Initially, the development of the shoot-to-plant ratio, based on the development of the n/c ratio, of the shedding plant was comparable to that of the plant that never sheds

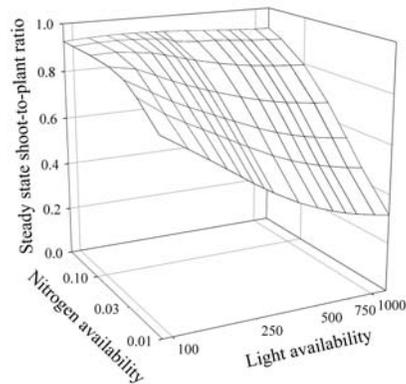


Figure 18 Effect of light and nitrogen availability on the steady state shoot-to-plant ratio of a plastic plant that never sheds its leaves.

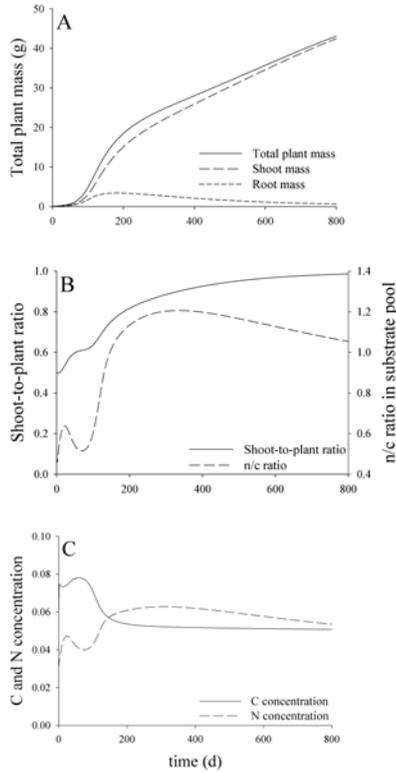


Figure 19 A) Total plant mass, shoot mass and root mass, B) Shoot-to-plant ratio and n/c ratio and C) C and N concentration in the substrate pool of a plastic plant that sheds its biomass, grown at high light intensity ($i_0 = 800 \mu\text{mol m}^{-2} \text{s}^{-1}$) and a nitrogen supply (n_s) of 0.01. Plasticity parameters: $\kappa = 2$, $\text{Max} = 4$, $\alpha = 1.2$.

it's biomass. After a decrease in shoot-to-plant ratio imposed by the low nitrogen – high light environment, the shoot-to-plant ratio increased again as maintenance respiration and self-shading increased in importance. However, this increase in shoot-to-plant ratio did not bend off to a constant as occurred in the non-shedding plant. Because the n/c ratio remained above v_{ref} and growth did not stop, the plant continued to increase its shoot-to-plant ratio. At the end of the simulation period, the n/c ratio in the substrate pool decreased. This was due to a decrease in the size of the belowground compartment because fine root mass was lost faster than new root mass was produced; consequently, nitrogen uptake decreased while nitrogen use, correlated with growth rate, did not change greatly and N concentration decreased (Figure 19C). This resulted in only a small change in the slope of the shoot-to-plant ratio graph. However, the n/c ratio did not decrease sufficiently to fall below v_{ref} hence the shoot-to-plant ratio kept increasing.

Analogous to the plant that never sheds its biomass, the shoot-to-plant ratio of the shedding plant is also affected by the environment. However, because this plant does not grow into a constant shoot-to-plant ratio and the shoot-to-plant ratio is thus very much dependent on the time at which the evaluation takes place, it is not possible to represent the effect of light and

nitrogen availability in a graph like the one presented in Figure 18. As can be observed from Figure 20 the shoot-to-plant ratio of the shedding plant, simulated in four different combinations of light and nitrogen availability, kept increasing at the end of the simulation. It can be expected that eventually the plant will, in all four environments, grow towards the maximum shoot-to-plant ratio, provided that it does not die of resource deprivation. As explained before, the extended simulation period used for the illustration and a better understanding of the general behavior of the model plant and the mechanisms that lie behind it, does not correspond to the length of a growing season. The growing season in this chapter is set to 150 days and the allocation behavior of the plastic plant should be evaluated over this time period, which is indicated in figure 20 by the dotted vertical line. In three of the four environments applied, the shoot-to-plant ratio started

increasing from the start of the simulation and remained increasing at $t=150$. This increase initially was brought about by a difference between C and N availability in the environment and the maintenance demands of the existing biomass, causing a high n/c ratio. For the species in the high light, high N environment, gradually another factor started playing a role. The leveling off of the gross photosynthesis combined with increasing maintenance respiration brought about a further decrease in the carbon concentration. This decreasing carbon concentration not only caused a further increase in the n/c ratio but also reduced the growth rate as a consequence of substrate limitation. Thus, the effect on the shoot-to-plant ratio, which was still increasing, did not differ from the other two environments, but the underlying processes responsible for the pattern were different. The shoot-to-plant ratio occurring in the fourth environment presented in Figure 20 decreased from the start due to the high availability of light in the environment and the low nitrogen availability.

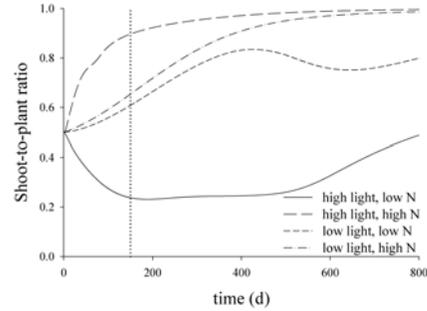


Figure 20 Effect of light and nitrogen availability on the shoot-to-plant ratio of a shedding plant. Light and nitrogen environments as presented in Figure 17. The dotted vertical line indicates the standard simulation period of 150 days.

From the above it can be concluded that the reference value of the n/c ratio v_{ref} , or, worded differently, the n/c ratio corresponding to the ratio in which nitrogen and carbon are demanded by the growth processes of the plant, should change in the course of the simulation period to promote optimal biomass production. After all, at the beginning of the simulation, as the plant is still small, the carbon demand is, relative to the N demand, not as high as later in the simulation, when self-shading and maintenance processes have

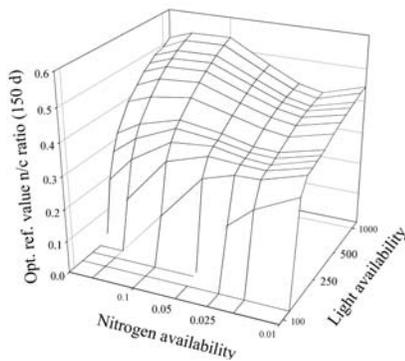


Figure 21 Optimal v_{ref} as a function of light and nitrogen availability for a simulation period of 150 days

increased in importance. Since implementation of a variable v_{ref} and evaluation of the optimum strategy would greatly enhance the complexity of the model and would complicate the comprehensibility, the value of v_{ref} is, for now, set to a fixed value over the simulation period. The optimum value of a constant v_{ref} is expected to be dependent on growth and maintenance demands over the simulation period, which dependent on the resource availability in the growth environment. Furthermore, resource availability in the environment is expected to also play a direct role in the determination of the optimum v_{ref} value, as well as the evaluation period. In

Figure 21 the optimal value of v_{ref} is presented as function of light and nutrient availability for four different evaluation periods. First the results of the standard simulation time of 150 days will be discussed, followed by an analysis of the effect of the simulation period. In general the optimum value of v_{ref} for a simulation period of 150 days was below 0.6 and decreased with decreasing light. This can be attributed to the direct effect of the light environment. With decreasing light, the need for aboveground biomass increased in order to increase the carbon gain, thus an allocation towards the shoot at lower values of n/c was profitable. Light had the largest effect on the optimum value and v_{ref} increased with increasing light availability.

The effect of nitrogen on v_{ref} was less straightforward. Analogous to the effect of light, the expectation was that the optimum value of v_{ref} would decrease with increasing nitrogen supply. After all, with increasing N availability, growth limitation of nitrogen will decrease and a lower reference value of the n/c ratio will bring about an allocation towards the shoot over a larger range of n/c ratios. However, this pattern was only found at low light levels; at high light level, starting at the lowest level of N availability, v_{ref}^* initially decreased with increasing N in the environment, in accordance with the expectation. Subsequently, v_{ref}^* increased and finally, at the highest N levels, decreased again. The unforeseen increase in v_{ref}^* can be attributed to the N demand of growth. At high light availability, growth can be fast. The higher the nitrogen availability, the faster growth was. However, as can also be concluded from Figure 11, the advantage of a slightly higher N availability for biomass production was large in this range of resource availability. So, although N availability was high, N demand to support this fast growth also was high. To maintain this fast growth, a high N concentration had to be maintained in the substrate pool. This could be attained by increasing the allocation towards the belowground compartment; v_{ref} increased. When N availability was set to even higher levels, biomass production slowed down due to the increase of self-shading. Although a large amount of nitrogen was still needed to support the fast growth, the carbon demands at the end of the simulation increased more strongly and so did the need for aboveground biomass. The reference value of the n/c ratio decreased again to facilitate allocation towards the shoot.

So, the optimal value of v_{ref} depends on the light and nitrogen availability in the simulation environment. However, plants are not capable of predicting the environment they grow up in. The question then is, what happens to the performance, i.e. total plant mass, if the plant has a non-optimal value of v_{ref} ? In Figure 22 the performance of the plants with different

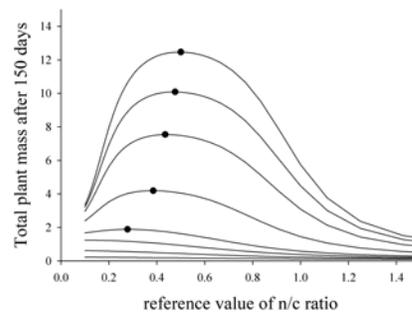


Figure 22 Total plant mass after 150 days over a range of v_{ref} values in different light environments and $n_a = 0.1$. The light availability in the environment is lowest for the bottom line and increases with plant mass, the dots on each line represent the optimum value of v_{ref}

values of v_{ref} , represented by the total plant mass after 150 days, is given. The different lines represent different levels of light availability; the nitrogen availability did not differ between the simulations. The optimum value of v_{ref} is given by the dots for each light level. The figure shows that a small deviation of v_{ref} did not have a large effect on plant performance; a deviation in v_{ref} of 15-25% percent still yielded 98% of the biomass at optimum v_{ref} .

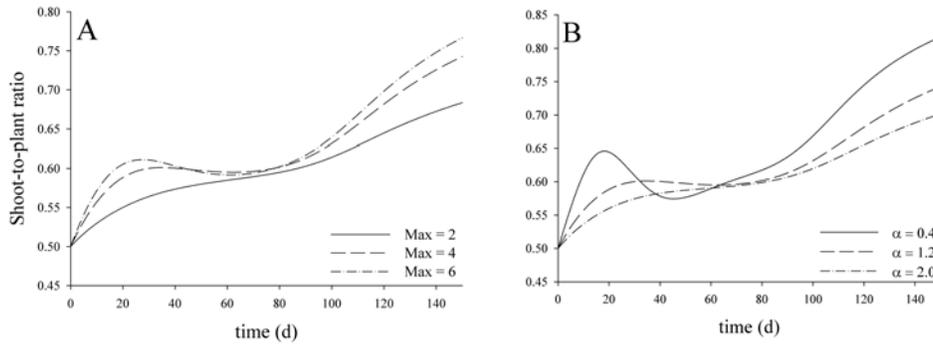


Figure 23 Effect of a change in allocation parameters A) α and B) Max on shoot-to-plant ratio.

The other two allocation parameters, Max and α , do not affect the proportional allocation; they affect the rate at which the shoot-to-plant ratio changes. The higher the value of Max, the faster the plant can adjust its shoot-to-plant ratio (Figure 23A). As explained before, when Max is set to the minimum value of 1, the plant has a rigid allocation strategy. The higher the value of α , the slower the plant adjusts its shoot-to-plant ratio, so the smaller the changes in σ during the simulations (Figure 23B). These parameters can thus be used to set the level of plasticity of different model species. In general, the faster the change in shoot-to-plant ratio, the higher the biomass productions over a 150 day period, but differences were small (data not shown).

DISCUSSION

A model is, by definition, a simplification of a system (Jørgensen & Bendoricchio, 2001). This simplicity represents the major strength of the use of models in the study of complex systems. It enables a stronger focus on the processes of interest and keeps the study system comprehensible. However, it is important that the model contains the characteristic features that are essential in the context of the problem to be solved or described (Jørgensen & Bendoricchio, 2001).

The model described in this chapter is developed to study the role of shoot-to-plant ratio and SLA on the whole-plant performance of plant species subjected to different light and

nutrient conditions. The ultimate goal is to understand how these plant traits affect the plant performance of different species groups of the forest understory in newly planted forests on former agricultural land. Because SLA and shoot-to-plant ratio are pointed out as central in the problem at hand, these two plant traits are major characteristics of the model plant and can be changed in order to define different species. Furthermore, the model consists of a simple, two-compartment (above and belowground), model plant that grows on carbon (C) and nitrogen (N). Water and other nutrients are not included. Both compartments are involved in one task only, the acquisition of either carbon or nitrogen. This construction of a two-compartment - two resource model has been commonly applied in plant growth modeling (e.g. Aikio & Markkola, 2002; Johnson, 1985; Thornley, 1972; VanderWerf *et al.*, 1993). Despite the unquestioned fact that real plants have many resources and many compartments, concentrating on C and N is not unreasonable because they are the major structural components of plants, their metabolism is suitably complex and interdependent, and their acquisition is associated with specific, spatially separated compartments (Cheeseman *et al.*, 1996).

For the resource acquisition calculations a realistic, though simple, light climate and nitrogen environment is used, in which the leaf and fine root biomass set gradients of resource availability within the two compartments. Consequently, the acquisition of carbon and nitrogen scales asymptotically with leaf and root mass. This approach is not followed in many allocation models. Often application of a constant acquisition rate per gram or area of above or belowground functional biomass is used (Marcelis *et al.*, 1998). Constant acquisition rates lead to exponentially growing plants, which are suitable for analyzing the effect of the environment on the shoot-to-plant ratio because all relative variables (e.g. concentrations and shoot-to-plant ratio) become constant. However, they cannot be used to simulate plant growth and allocation realistically. The results presented in this chapter show that the resource demand of the plant changed over time, with the size of the plant. As the plant increased in biomass, self-shading and maintenance processes increased in importance and carbon demand increased, while the demand of N, solely required in growth processes, decreased with increasing biomass and decreasing growth rate (e.g. Figure 8 and Figure 10). The change of the plant over time in turn was determined by the resource availability in the environment.

Since the plastic plant could adjust its allocation to its resource needs the steering of biomass allocation also changed over time. As carbon demands increased with increasing plant mass, the allocation towards shoot mass increased (Figure 15, Figure 17, Figure 19 and Figure 20). This is consistent with the results of e.g. Poorter *et al.* (1988), who found an increase in shoot-to-plant ratio as self-shading increased with the size of *Plantago major* plants. Furthermore, models assuming exponential growth analyze the shoot-to-plant ratio in the steady state situation and do not study the development of the shoot-to-plant ratio as a function of time. The simulation results presented in this chapter showed that in the evaluation time plays an important role in the relation between shoot-to-plant ratio and environment.

Discussion

The importance of evaluating leaf functional traits on the whole plant level is illustrated in Figure 12. A different ranking in terms of biomass production between plants with different values of SLA and correlated traits was found in the beginning of the simulation period, when whole-plant processes like self-shading and maintenance respiration did not yet play an important role, as compared to the end of the simulation period.

Storage and reproduction are not considered, but the model can easily be extended with these functions.

Because of a future extension to a competition model, the model should also show a realistic height growth pattern, in which different strategies with different costs for support can be created. As is shown in Figure 14 height growth of the plant entails carbon and nitrogen costs for the production of supportive biomass; resources that cannot be invested in carbon and nitrogen acquiring functional biomass, thus affecting total plant production.

APPENDIX I CONVERSION OF LONGEVITY TO BIOMASS LOSS RATE

The conversion of leaf longevity to leaf loss rate is based on a standard exponential decay model (Yodzis, 1989),

$$M_L = M_0 \cdot e^{-\tau \cdot L} \quad (I.1)$$

with τ the loss rate of leaf or fine root mass in gram shed biomass per gram existing biomass per day, M_0 is either the leaf mass or the fine root mass at the moment of production in gram dry weight, $M_{(L)}$ is the leaf mass or fine root mass that is left after L days in gram dry weight.

The biomass that is left after L days $M_{(L)}$ can be expressed as the $1/k$ fraction of M_0 ,

$$M_L = \frac{1}{k} \cdot M_0 \quad (I.2)$$

By assuming M_L , the fraction of M_0 that remains after L days to be very small, thus k being very large, L can be defined as approximating the longevity of biomass. Substitution of Equation I.2 into Equation I.1 leads to:

$$\frac{1}{k} = e^{(-\tau \cdot L)} \quad (I.3)$$

Then biomass loss rate τ can be described as function of longevity L ,

$$\tau = \frac{\log(k)}{L} \quad (I.4)$$

Longevity of leaf biomass (LL) is assumed to be a function of Specific Leaf Area (SLA), which is described by:

$$\log(LL) = a_L - b_L \cdot \log(SLA) \quad (I.5)$$

where a_L and b_L are parameters to shape the relation.

Because biomass loss τ_a is a function of longevity and longevity is a function of SLA , biomass loss can be expressed as a function of SLA .

$$\log(\tau_a) = \log(\log(k)) - \log(LL) \quad (I.6a)$$

$$\log(\tau_a) = \log(\log(k)) - (a_L - b_L \cdot \log(SLA)) \quad (\text{I.6b})$$

$$\tau_a = \log(k) \cdot e^{-a_L} \cdot SLA^{b_L} \quad (\text{I.6c})$$

APPENDIX II HEIGHT-STEM MASS RELATION

The height-stem mass relations used in the model is based on Greenhill's formula of the critical buckling height (Niklas, 1995), which describes the biomechanical constraints of height growth and results in an increasing stem diameter with increasing height.

$$H = \alpha \cdot D^\beta \quad (\text{II.1})$$

where H is the height of the stem in meter, D is the diameter of the stem in meter, which is assumed to be constant over height, and α and β are parameters to shape the relation.

Stem mass is calculated from the density of the stem tissue ρ and the volume of the stem,

$$M_{aS} = \rho \cdot \pi \cdot r^2 \cdot H \quad (\text{II.2})$$

where r the radius of the stem in meter.

To express H as function of M_{aS} , stem radius r is solved from II.1, i.e. substituting D with 2r results in:

$$H = \alpha \cdot (2r)^\beta = \alpha \cdot 2^\beta \cdot r^\beta \quad (\text{II.3})$$

Thus, radius r can be written as function of height,

$$r^\beta = \frac{H}{\alpha \cdot 2^\beta} \quad (\text{II.4})$$

$$r = \left(\frac{H}{\alpha \cdot 2^\beta} \right)^{1/\beta} = \left(\frac{1}{\alpha} \right)^{1/\beta} \cdot \frac{1}{2} H^{1/\beta} \quad (\text{II.5})$$

Substitution of r into Equation II.2 leads to:

$$M_{aS} = \rho \cdot \pi \cdot \left(\left(\frac{1}{\alpha} \right)^{2/\beta} \cdot \frac{1}{4} H^{2/\beta} \right) \cdot H \quad (\text{II.6a})$$

$$= \frac{\rho \cdot \pi}{4} \cdot \frac{1}{\alpha^{2/\beta}} \cdot H^{1+2/\beta} \quad (\text{II.6b})$$

From this equation the height-stem mass relation can be derived:

$$H^{1+2/\beta} = \frac{4\alpha^{2/\beta}}{\rho \cdot \pi} \cdot M_{aS} \quad (\text{II.7a})$$

$$H = \left(\frac{4\alpha^{2/\beta}}{\rho \cdot \pi} \right)^{\beta/(\beta+2)} \cdot M_{aS}^{(\beta/(\beta+2))} = k \cdot M_{aS}^{(\beta/(\beta+2))} \quad (\text{II.7b})$$

with:

$$k = \left(\frac{4\alpha^{2/\beta}}{\rho \cdot \pi} \right)^{\beta/(\beta+2)}$$

Chapter 3

Shade tolerance: the role of leaf functional traits and biomass allocation

ABSTRACT

The capability of plant species to grow at low light availability has interested ecologists for many years. Recently it has been suggested that a conservation strategy, characterized by minimization of biomass loss and maintenance respiration rates, both associated with a low Specific Leaf Area (SLA), plays a central role in shade-tolerance. Furthermore, shade-tolerant species should invest a larger part of their biomass in light harvesting biomass than in nitrogen acquiring biomass; in this trait the between-species pattern is expected to correspond to the plastic response to environmental conditions, widely described in past studies. In this study, the above presumptions are tested in a modeling study. Analyzing the traits that support the highest net biomass production at different light availability. Furthermore, it was tested how species should adapt to conditions where light availability is not low constantly but only later in the growing season, like is the case in a deciduous forest.

The model simulations showed that at low light availability the conservation strategy, represented by a low SLA, resulted in the highest net biomass production over the growing season. The role of minimization of biomass loss and maintenance respiration rates decreased with increasing light availability. The same pattern was found at light regimes mimicking a deciduous forest. The between-species pattern in adaptation of shoot-to-plant ratio to different growing environments, both at constant and at varying light availability, also was as expected. At low light (minimum) conditions a higher shoot-to-plant ratio was found to be most profitable, at higher (minimum) light availability a lower optimal shoot-to-plant ratio was found. These results support the hypothesis that conservation of acquired resources and a high shoot-to-plant ratio are a characteristic of shade-tolerance, even if light conditions are low only part of the season.

Keywords: growth strategy, leaf functional traits, mechanistic plant growth model, shade-tolerance, shoot-to-plant ratio

INTRODUCTION

The adaptation of plant species to their growing conditions has interested ecologists for many years. In this context the capability of plant species to grow at low light availabilities has received much attention. A conceptual model of shade tolerance, that was popular for a long time, assumed that tolerant species would have the physiological and morphological traits that allow for higher growth rates under low light conditions than shade-intolerant species would be able to. These traits include greater Specific Leaf Area (leaf area per unit leaf mass, SLA) and mass-based photosynthetic capacity (A_{mass} ; see Walters & Reich, 1999). Within-species plastic responses to a decrease in light availability are indeed characterized by an increase in SLA (e.g. Bungard *et al.*, 1998; Evans & Poorter, 2001, Onimaru & Yabe, 1996; Shipley, 2000).

When comparing among species the above concept may not apply. For example, Walters and Reich (1999) demonstrated that young seedlings of shade-tolerant species do not achieve higher net carbon gain than shade-intolerant species. The same result was found in a study on the growth of tropical tree seedlings in contrasting light environments (Veneklaas & Poorter, 1998). Apparently, shade-tolerant species do not maximize their SLA and A_{mass} at all cost (Veneklaas & Poorter, 1998). These two traits are part of a suite of correlated traits based on physical, physiological and bio-mechanical constraints that has extensively been studied (see Ackerly & Reich, 1999). For instance, SLA has been shown to be positively correlated to the loss of leaf biomass in a variety of habitats (Reich *et al.*, 1992, 1997; Westoby *et al.*, 2000). Low-SLA leaves generally are thicker, physically more tough and tend to have larger amounts of secondary chemical defenses (Ninnemets, 1999; Westoby *et al.*, 2000, 2002; Wilson *et al.*, 1999) and thus have a lower loss rate. Because a large share of the respiration costs is involved in the periodic (and costly) re-synthesis of the enzymes of the photosynthetic complex, maintenance respiration rate, R_m , has been positively related to mass-based photosynthetic capacity, A_{mass} (Field & Mooney, 1986; Meziane & Shipley, 2001; Reich *et al.*, 1992, 1998a, 1998b). In addition, since leaf nitrogen is a primary component of photosynthetic enzymes, the photosynthetic capacity and maintenance respiration rate are positively correlated with n_c , the leaf nitrogen concentration (Field & Mooney, 1986; Evans, 1989). Furthermore, low SLA-leaves have a greater allocation to structural rather than metabolic components. A low SLA thus is correlated with low R_m , A_{mass} and n_c ; a high SLA with high R_m , A_{mass} and n_c .

Apparently, two opposite strategies can be distinguished; a plant can either produce leaves that possess a high photosynthetic assimilation rate with high maintenance costs that persist briefly, or provide a resistant leaf physical structure with lower photosynthetic capacity and a smaller light capturing area per unit of leaf dry mass (SLA) resulting in a lower carbon assimilation rate but over a longer period of time (Reich *et al.*, 1992). For simplicity these two strategies are referred to as the high- and low-SLA strategy, respectively. Walters and Reich (1999) suggested that the low-SLA strategy characterizes shade-tolerance, and ascribed a central role to minimization of biomass loss and

maintenance respiration rates, related to a low SLA, in adaptation to low light conditions. Production of leaves with high photosynthetic capacity would then be more favorable under higher light conditions. Unfortunately, besides the studies mentioned, there are few data that support this hypothesis. Moreover, the consequences of the suite of correlated traits on whole-plant performance under different environmental conditions have not been analyzed in a quantitative way.

To understand the role of SLA and correlated traits in plant growth a quantitative link between those traits and the performance of plant species in terms of growth or reproduction has to be made. A suitable method to approach this problem and focus on the plant traits of interest is a modeling approach. In this chapter a biologically realistic model will be used to analyze if a low SLA and correlated traits, representing a biomass conservation strategy, leads to the highest net seasonal biomass production under low light conditions, while at higher light conditions the opposite set of traits will be more beneficial. The model includes the correlated trait relations as presented in the work of Reich and co-workers (Reich *et al.*, 1992; Reich *et al.*, 1998a; Reich *et al.*, 1998b).

The assumption that the low-SLA strategy is an adaptation to low resource availability raises the question what strategy should be followed in a habitat where resources are scarce during only part of the growing season, like the understory of a deciduous forest. Will the higher light availability at the beginning of the growing season release the need for biomass conservation or will production of leaves with a short lifespan, that thus have to be replaced during the season, and high maintenance costs negatively impact plant performance later in the season when light availability is low? By applying a variable light climate in the model simulations, the effect of temporal low light conditions on the performance of plant species differing in SLA and correlated traits will be analyzed.

The net biomass production of a plant not only depends on leaf functional traits but also on its capability to acquire its growth resources in proportion to its needs. To maximize growth, the division between aboveground carbon capturing biomass and belowground nitrogen capturing biomass should be in balance with the ratio between light and nitrogen availability in the environment. Within-species plastic responses to changes in resource availability in their environment have been widely described and there is general agreement on the patterns (e.g. Brouwer, 1962a; Bungard *et al.*, 1998; Ericsson, 1995; Olff *et al.*, 1990; Poorter & Nagel, 2000). In general, species tend to shift their biomass allocation towards aboveground biomass when light is limiting and, similarly, when growth is impaired by nutrient availability a shift towards belowground biomass is found. Between-species differences also have been subject to study (e.g. Körner, 1994). In contrast to the expected difference within and between species with regards to SLA and correlated traits, the between-species pattern in shoot-to-plant ratio in relation to the resource availability in the environment is not expected to differ from the within-species response to light and nitrogen availability. Since the shoot-to-plant ratio in the model described above is quantitatively related to the performance of the plant, this hypothesis

can also be tested with the model. Following the above line of reasoning, when light availability decreases during the growing season, resembling a deciduous forest understory climate, light availability at the beginning of the growing season will select for a low shoot-to-plant ratio. This will have consequences for plant growth in the low light phase later in the season. The maintenance costs of the total plant mass that is produced during the high-light conditions may weigh heavy on the carbon budget in the low light period and growth will slow down or even become negative. This may not only select for a higher shoot-to-plant ratio to be able to pay for the maintenance costs in the low-light period but also reduces the growth rate in the initial high-light period. Thus, maximization of the growth rate in the high light phase is expected to have a negative effect on plant growth over the full season.

To summarize, in this chapter four topics will be addressed. First, the suggestion that the between-species response to shade is opposite to the within-species response is tested by analyzing the consequences of the suite of correlated leaf functional traits for the whole-plant performance under different environmental conditions, in our model represented by SLA. Next the effect of a variable light regime, mimicking the light climate in a deciduous forest understory, on the relation between SLA and plant performance is tested. Then the effect of resource availability on the shoot-to-plant ratio achieving the highest net biomass production is analyzed to test if the between-species pattern corresponds to the within-species pattern. And, finally, the effect of a variable light regime on the optimal shoot-to-plant ratio is tested.

These questions are addressed using a biologically realistic growth model. Light capture and belowground resource acquisition are modeled in a realistic fashion, including self-shading aboveground and resource depletion belowground. As a consequence mass-based uptake rates of light and N decrease with plant size. The model therefore does not assume exponential growth and is not restricted to the earliest part of the growing season. A detailed description of the model is given in the previous chapter.

METHODS

MODEL DESCRIPTION

In this chapter two models are used, an analytic model and a mechanistic simulation model. The analytic model encapsulates the key processes of plant growth and describes the essence of the system in a limited number of equations. The mechanistic model comprises processes and plant characteristics that enable a more biologically realistic simulation of plant growth. Together the results of the two models clearly describe the effect of leaf functional traits on plant performance and explain the mechanisms behind it. For the analysis of biomass distribution on plant performance, only the mechanistic model was used.

The analytic model can be used to analyze the Relative Growth Rate (RGR) of plants differing in leaf functional traits. The RGR results from a simplified biomass production function and a turnover function. The simplified biomass production function calculates gross biomass production from the net carbon acquisition rate and the carbon investment needed per unit new biomass. Net carbon acquisition rate is determined by the relative amount of photosynthesizing biomass, in this analytic model defined as the total aboveground biomass, the photosynthetic carbon gain rate of this biomass (A_{mass}) and the respiration rate of the total plant mass (R_m). A complete description of the analytic model is given in the Appendix of this chapter. Results are described based on a visual representation of the model shown in Figure 1.

As a consequence of the application of the correlated traits relations, A_{mass} and R_m are functions of SLA, which resulted in a gross biomass production curve that increased with increasing SLA (solid lines in Figure 1). The biomass production is a function of light intensity (Figure 1A) and shoot-to-plant ratio (Figure 1B and C). Also based on the suite of correlated traits, biomass loss rate (τ) is a concave increasing function of SLA (bold lines in Figure 1). This relation is not dependent on light intensity and shoot-to-plant ratio. The RGR is the difference between biomass production curve and biomass loss curve.

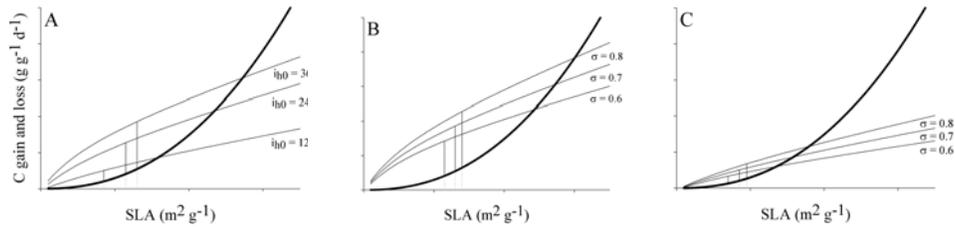


Figure 1 Representation of the visual model. The bold line represents the relative leaf loss rate (τ), the other lines the relative biomass production rate (μ) for different values of A) light (i_0), B) shoot-to-plant ratio (σ) at low light conditions, and C) shoot-to-plant ratio at high light conditions. The straight vertical lines indicate the optimum value of SLA.

A complete description of the simulation model used in this chapter is given in Chapter 2. The model plant consists of aboveground stem and leaf mass and belowground fine and coarse roots. Newly produced functional biomass, leaves and fine roots, is placed at the top of the aboveground or at the bottom of the belowground plant part, thus requiring production of stem and coarse root to support the increase in height. Plant growth is driven by carbon (carbohydrates) produced in photosynthesis by the leaves and nitrogen (amino-acids) taken up by the roots. The model explicitly considers light extinction within the canopy of the plant and therefore light availability in the lower layers of the canopy decreases with the leaf area of the plant, as is described by Beer's law (Johnson & Thornley, 1984; Monsi & Saeki, 1953), and gross photosynthetic rate per gram leaf consequently goes down. Comparably, with increasing root biomass, N availability in the depletion zone decreases and N uptake rate per gram fine root decreases as well. Acquired

Table I Correlated trait relations, parameters settings and literature sources.

Relation	
1	$\log(LL) = -2.16 - 2.326 * \log(SLA)$
2	$N_{si} = 0.02025 + 0.77 * SLA$
2	$P_{gm} = -0.0115 + 9.23 * N_{si}$
3	$R_m = -0.023 + 0.12 * P_{gm}$

1 Reich *et al.* (1992)

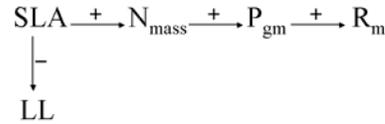
2 Reich *et al.* (1998a)

3 Reich *et al.* (1998b)

C and N are first stored in a substrate pool and from there used for plant growth and maintenance respiration.

The growth rate depends on the availability of carbon and nitrogen in the substrate pool. If both resources are in ample supply the maximum growth rate is reached. When the supply of either one or both of the

resources in the substrate pool is low, growth rate is reduced. Only functional biomass, leaves and fine roots, is shed during the simulation period. Supportive biomass (stems and coarse roots) is not lost from the plant. The functional biomass is lost at a constant shedding rate, which is correlated with the Specific Leaf Area. This relation is part of a suite of correlated leaf functional traits that forms the basis of species definition in this chapter (Reich *et al.*, 1992; Reich *et al.*, 1998a; Reich *et al.*, 1998b). Other characteristics in the suite of correlated traits are leaf nitrogen concentration ($[N_{mass}]$), mass-based photosynthetic capacity (P_{gm}) and maintenance respiration rate (R_m). The constant shedding rate is derived from the leaf longevity (LL) as is explained in Chapter 2. The correlated scheme is given below and the exact relations are given in Table I.



As explained in the introduction, SLA is negatively correlated to LL and positively to N_{mass} . N_{mass} is positively correlated to P_{gm} which, in turn, is positively correlated to R_m . In the simulations a rigid model plant species, not capable of adjusting its biomass allocation to its resource demands, was used. Parameter settings are presented in Table II.

The environment in which the model plant grows can vary in light and nitrogen availability. The nitrogen supply in the ambient soil is set at the beginning of the simulation period and is constant during the simulation. Nitrogen availability in the depletion zone results from transport processes in the soil and N uptake by plant roots. Light availability can be set to a constant level during the simulation period but can also be set to a variable light regime, mimicking the light availability in a deciduous forest. In the simulates deciduous forest conditions the light regime starts at a high light availability that decreases rapidly from the beginning of the growing season to a chosen lower light level; thus simulating the rapid decline in light availability that occurs in deciduous understories in spring when canopy leaves expand. More information about the deciduous light regime can be found in the model description and in Figure 7 of Chapter 2.

SELECTING THE OPTIMAL PLANT TRAITS

The total plant biomass at the end of the simulation period of 150 days is used as a measure of plant performance. This total plant biomass can be viewed as the result of growth and shedding processes as explained above and in Chapter 2.

Four sets of simulations for selecting the optimal plant traits can be distinguished (Table III). First, plant performance was studied as a function of SLA as a representative of the suite of correlated traits (given in Table I). The SLA at which the total plant biomass at the end of the simulation period was highest, is referred to as the optimal SLA or SLA*. SLA is assumed to be constant during the course of the growing season. This approach is applied to different constant light levels (Photosynthetic Active Radiation, PAR) at the top of the model plant over a range from 30 to 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which represents 2 to 66% of the light that is available above the forest tree canopy on a clear day in temperate regions. Furthermore two levels of nutrient availability are simulated. This set of simulations is repeated for different values of shoot-to-plant ratio (σ).

To analyze the effect of parameter settings of the correlated trait relations on the outcome of the simulations, the set of simulations was repeated with a 10% change in the relations presented in Table I.

Second, the effect of a variable light regime, mimicking the light availability in the understory of a deciduous forest, on the SLA was studied (simulation set B). The above-described method was repeated with a series of variable light regimes. Light intensity at the beginning of the growing season was kept constant on 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and minimum light availability later in the season was varied over a range of 30 to 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

For the last two sets of simulations, to determine the optimal shoot-to-plant ratio (C and D in Table III), the same approach was followed. Optimal shoot-to-plant ratio was defined as the shoot-to-plant ratio at which the highest total plant mass was reached after 150 days. Optimal shoot-to-plant ratio was studied at different values of SLA.

Table II List of standard parameter settings and literature sources.

Abbreviation	Value	Unit
r_{nu}	*	0.00125 $\text{g g}^{-1} \text{d}^{-1}$
c_c	*	0.8 g g^{-1}
n_r	¹	0.014 g g^{-1}
k_c	*	0.2 g g^{-1}
k_n	*	0.05 g g^{-1}
c_{min}	*	0.05 g g^{-1}
n_{min}	*	0.01 g g^{-1}
c_{leth}	*	0.001 g g^{-1}
n_{leth}	*	0.001 g g^{-1}
k	*	0.02 -
r_{ac}, r_{bc}	*	0.075 m
ρ_{MAL}, ρ_{MBR}	*	3000 g m^{-3}
k_H	*	0.25 -
β	*	1.279 -
a_L	²	0.82 -
α_L	³	20 rad
Φ	⁴	0.05 $\mu\text{mol } \mu\text{mol}^{-1}$
θ	⁴	0.8 -
R_{nc}, R_{nd}	*	0.1 d m^{-1}
k_{nd}	*	0.0714 -
p	*	1 -
p_n	*	5 -

* estimated
 ** mathematical parameter
¹ Aerts (1996)
² Rosati et al. (2001)
³ Schieving (1998)
⁴ Anten (1995)

SIMULATION RESULTS

OPTIMAL SLA AT CONSTANT LIGHT AVAILABILITY

First, plant performance was studied as a function of SLA and correlated traits in an environment with constant given light availability of $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 2). A low SLA and hence low biomass loss, photosynthetic capacity and maintenance respiration rate, resulted in a low total plant mass. Also at high SLA, associated with high values of the leaf functional traits, performance was low. As expected, an optimum was found in between. The mechanism behind this pattern can best be explained with the visual representation of the analytic model (Figure 1). The highest biomass production over the growing season is assumed to be at the SLA where RGR is maximal. This SLA is indicated by the vertical lines in Figure 1. If SLA was below the optimal value, both

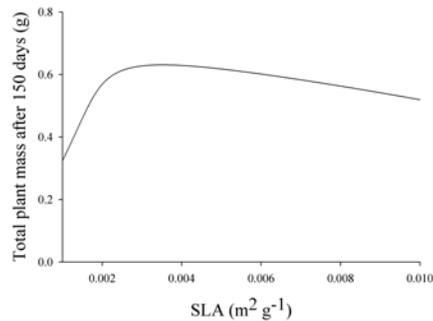


Figure 2 Plant performance in terms of total plant mass after 150 days over a range of SLA-values at high light availability ($600 \mu\text{mol m}^{-2} \text{s}^{-1}$). SLA is correlated to mass-based nitrogen content, photosynthetic capacity, and maintenance respiration rate, as well as to leaf longevity.

production and loss of biomass were low, resulting in a low plant performance. A SLA above the optimum did bring about a higher biomass production rate but this was counteracted by a high rate of biomass loss in shedding processes, thus decreasing the difference between the biomass production rate and biomass loss rate.

The simulation model was used to determine the optimal SLA values numerically for a range of light intensities and plotted as a function of light (Figure 3). As expected, the model predicted a low SLA^* , connected to low biomass loss and low maintenance costs, at low light conditions. With increasing light availability, SLA^* increased, more and more

representing a suite of traits that is aimed at high carbon acquisition at the cost of traits connected to conservation of biomass and reduction of maintenance costs. After a steep increase in SLA^* with light, a maximum was reached and SLA^* started decreasing with further increasing light intensity.

Just as the plant performance as a function of SLA, this pattern can also be explained by using the visual representation of the analytic model. In Figure 1A the biomass production at three different light intensities is shown. At low light availability, biomass production was slow and only at low values of SLA, associated with low shedding rates, could a positive RGR be reached. As light availability increased, a higher gross photosynthesis could be reached, resulting in a higher biomass production rate, while the biomass loss curve did not change. The largest difference between the τ -curve and the μ -curve, and thus the optimal value, moved to a higher SLA.

Results

The analytic model predicted an ever-increasing SLA^* with increasing light availability. This does not comply with the predictions of the simulation model that showed an increase in SLA^* only in the low light range and a decrease in SLA^* at higher light availabilities. This difference can be ascribed to self-shading. A higher light intensity favored growth resulting in larger plants and more severe self-shading. Would the plant from the simulation model keep increasing SLA , the larger leaf area would imply a greater degree of self-shading and gross photosynthesis per gram biomass would decrease, in spite of the higher capacity connected to the higher SLA . Since maintenance respiration rate is also positively correlated to SLA , the higher maintenance respiration of a higher SLA would impose a double negative effect on the plant's net photosynthesis. Consequently, at the higher light intensities, the simulation model predicted low SLA values to diminish self-shading. Because self-shading is not included in the analytic model, an increase of the SLA in that model did not bring about any negative effects.

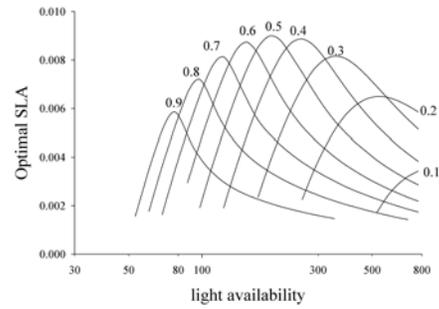


Figure 3 Optimal SLA over a range of constant light availability for a range of shoot-to-plant ratios, as indicated by the numbers above the lines.

Figure 3 shows the effect of shoot-to-plant ratio on the optimal SLA at a certain light intensity. Species with high values for σ achieved positive growth at the lowest light intensities; species with very low σ -values could only attain positive growth in the higher light range. At very low light conditions, SLA^* increased with increasing σ ; when more aboveground biomass was available, the need for conservation of energy and biomass decreased. At higher light intensities, the pattern is more complicated. For plants with higher shoot-to-plant ratios the ranking in SLA^* became opposite to the patterns found at low light conditions; the optimal SLA decreased with increasing σ . For plants with lower shoot-to-plant ratios, the optimal SLA increased with increasing σ conform the pattern found at low light conditions in the high σ -range.

Again, the analytic model can contribute to a better understanding of the mechanisms that generated the above-described pattern. In Figure 1B the biomass production rate for species differing in σ in a low-light environment is given as function of SLA (σ increasing is in the direction of the arrow). Due to a higher photosynthesizing biomass in the high- σ species, a higher gross carbon acquisition could be reached in this species, resulting in a higher biomass production rate at a given value of SLA , photosynthetic capacity and maintenance respiration rate. If gross biomass production rate was higher, the μ -curve crosses the τ -curve at higher SLA and the relative weight of the turnover rate in the calculation of the RGR decreased resulting in a higher value for SLA^* . For the same reason, the analytic model predicted an increasing SLA^* with increasing σ at high light

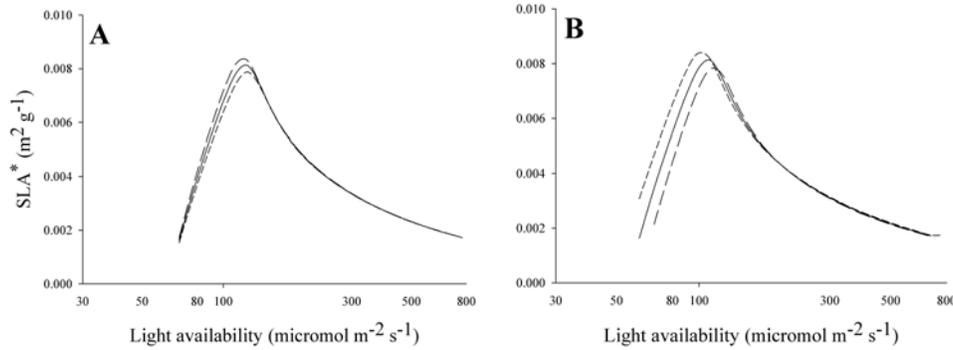


Figure 4 Effect of a 10% change in A) leaf longevity and B) mass-based maintenance respiration rate on the selection of the optimal SLA for with $\sigma = 0.7$. The solid lines represent the optimal SLA at the standard correlated trait relations shown in Table II, the long-dashed lines the optimal SLA when leaf longevity or maintenance respiration rate is increased with 10% and the short-dashed lines show the results of a 10% decrease in longevity or respiration rate.

intensity (Figure 1C). However, in the simulation model, the occurrence of self-shading, that is more severe in high- σ species due to larger shoot biomass, caused the ranking to reverse at high light availabilities.

To summarize the results described above, at low light availability, low values of SLA favored biomass production. With increasing light intensity, optimum SLA values first increased but then decreased again. Shoot-to-plant ratio was positively related to optimum SLA at low light availability, but at high light availability this effect was only found for species with low σ . For species with high σ , at high light levels shoot-to-plant ratio was negatively related to optimum SLA.

Two traits are assumed to play a role in the conservation strategy found at low light conditions: biomass loss rate (τ) and mass-based maintenance respiration rate R_{m-mass} . It is interesting to see if either one of those traits has a larger impact on the selection of the optimal SLA. To investigate this the effect of a 10% increase (long-dashed) or decrease (short dashed) of leaf lifespan (Figure 4A) and maintenance respiration rate (Figure 4B) on SLA^* was simulated.

In general, the pattern described above was only quantitatively and not qualitatively altered by a change in either of the two correlated trait relations. At the lowest light intensities, a change in leaf longevity had a small effect (3-5%) on the selection of the optimal SLA. This effect gradually disappeared with increasing light intensity. The effect of a change in maintenance respiration on the selection of SLA^* was larger. At low light intensities, a 10% change in respiration rate caused a 30 to 50% change in SLA^* . This effect decreased with increasing light intensity. At the highest light intensities, maintenance respiration rate no longer shaped the SLA^* -curve and the role of a change in respiration rate is negligible. In Figure 4 the results of the simulations with $\sigma = 0.7$ are

shown; the results at other values of shoot-to-plant ratio showed the same pattern. A change in photosynthetic capacity (A_{mass}) and nitrogen concentration (n_c), up to a 50% deviation in slope or intercept, also did not affect the optimal SLA pattern qualitatively.

OPTIMAL SLA AT VARIABLE LIGHT

When light availability was scarce only in the second part of the growing season the SLA*-curve changed compared to that at constant light. In Figure 5 both the optimum SLA at variable light regimes and at constant light are presented. The light availability on the x-axis represents the light intensity during the total simulation period for the constant light regime and the low light intensity occurring later in the simulation, for the variable light regime.

The SLA* found at the variable light regime was lower than the SLA* at constant (low) light. Especially around a (minimum) light availability of 100-200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ the differences were large. The lower optimal

SLA at variable light was brought about by a combination of several processes, all related to the trait correlation scheme. This can be illustrated using Figure 6 which shows the total plant mass (A), carbon and nitrogen concentration (B and C) and net and gross biomass production (D and E) at variable light climate of a species with the optimal SLA in this light regime and a species with the higher optimal SLA of the constant light regime. At first, only a small difference in total plant mass was found; after 20 days both plants have approximately the same biomass. However, a small difference persisted to the disadvantage of the species with the higher SLA. Figure 6B and C teach that this can be attributed to the N availability in the substrate pool that decreased faster for the high-SLA species than for the species with the lower SLA. This factor underlies the lower gross biomass production rate of the high SLA-species between day 10 and day 20 illustrated in Figure 6D. The stronger decline of the N concentration of the high-SLA species can be attributed to the correlation of a high SLA to a high leaf N concentration. One gram of biomass was more expensive in terms of N for the high SLA-species than for the low-SLA species. At low light conditions, the high-SLA species will not encounter this problem since growth was much slower and thus nitrogen demand lower. After approximately 50 days, the gross biomass production of the high-SLA species crossed that of the low-SLA species but still the total plant mass of the high-SLA species did not catch-up with that of the low-SLA species. Here the higher biomass loss rate comes into

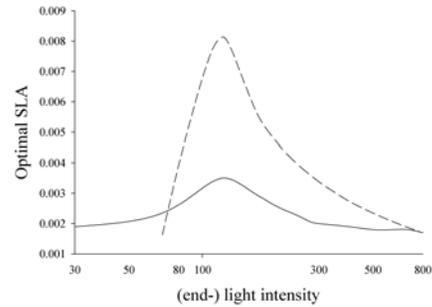
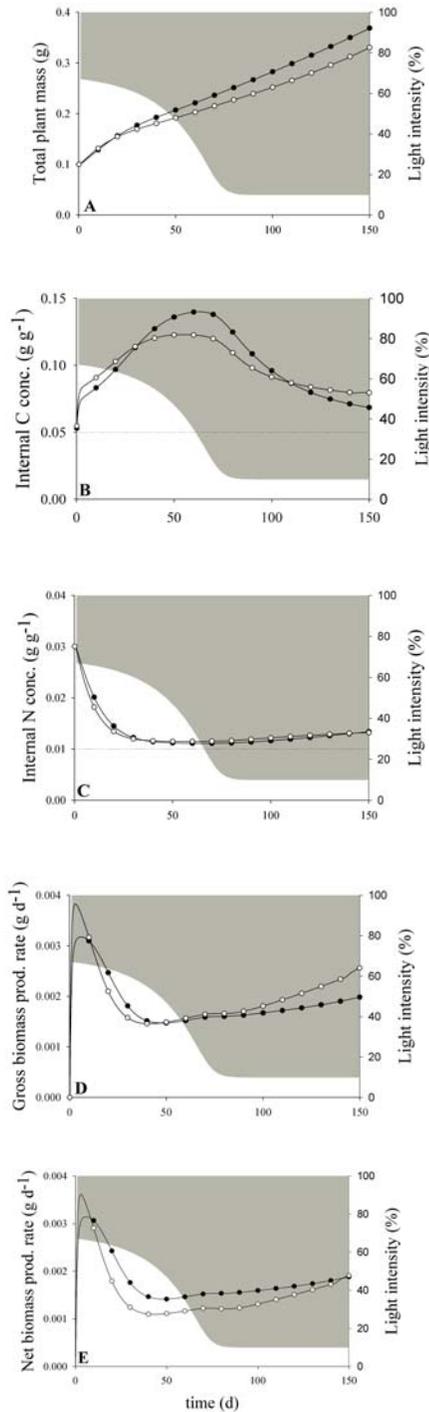


Figure 5 Comparison of the optimal SLA in a constant (dashed line) and a variable (solid line) light regime. For the simulations performed at the variable light regimes the light intensity on the x-axis represents the low light intensity later in the growing season.



sight. While gross biomass production rate of the high-SLA species was higher, net biomass production rate remained below that of the low SLA-species.

The higher the shoot-to-plant ratio, the flatter the SLA* -curve at variable light (data not shown). A higher σ resulted in a faster initial growth, as self-shading in this stage did not yet play an important role. The higher total plant mass did aggravate the slowing down of the initially steep increase in plant growth. The effect of maintenance respiration rate on gross biomass production, as described above, was amplified by the larger biomass that had to be maintained. If shoot-to-plant ratio was lower, growth was slower and the balance between biomass production and loss in the low light period played a more important role in the determination of the optimal SLA.

OPTIMAL SHOOT-TO-PLANT RATIO

Figure 7 shows the plant performance as a function of shoot-to-plant ratio (σ) at constant light availability. Biomass production in these simulations was determined by resource limitation (C and N). At low shoot-to-plant ratio, growth was impaired by carbon (C) availability, due to small aboveground biomass and thus constrained carbon acquisition. When shoot-to-plant ratio was high, nitrogen (N) uptake was low due to small belowground mass, and consequently nitrogen was limiting

Figure 6 Comparison of the total plant mass (A), the carbon (B) and nitrogen (C) concentration in the substrate pool, and the gross (D) and net (E) biomass production rates at variable light regime (minimum light intensity $120 \mu\text{mol m}^{-2} \text{s}^{-1}$) of a species with the optimal SLA in this light regime (filled circles) and a species with the optimal SLA found at constant light (light intensity $120 \mu\text{mol m}^{-2} \text{s}^{-1}$; open circles). The shades in the background represent the decrease in light availability during the simulation period.

Results

growth. The highest biomass was reached at the shoot-to-plant ratio where the balance between C and N limitation resulted in the highest biomass production rate for the largest part of the growing season.

The optimal σ was determined for a range of light intensities and plotted as a function of light (Figure 8). To illustrate the effect of nitrogen availability (N_a) and SLA on the pattern, simulations were repeated for different values of N_a and SLA. The effect of light on the optimal σ was as expected; a high light availability selected for a low σ and σ^* increased with decreasing light

availability. At very low light intensities, no optimum was found, and total plant mass after 150 days kept increasing with increasing shoot-to-plant ratio until the maximum value, set to 0.99, as σ cannot be larger than 1, was reached. In this low light environment,

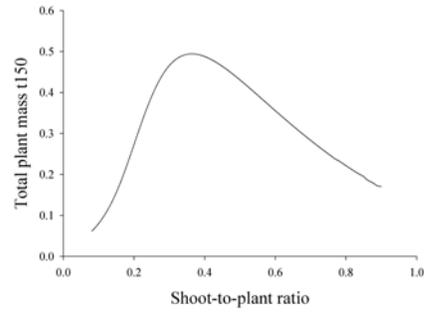


Figure 7 Plant performance in terms of total plant mass after 150 days over a range of shoot-to-plant ratios at high light availability ($i = 600 \mu\text{mol m}^{-2} \text{s}^{-1}$) and low n_a ($n_a = 0.01$).

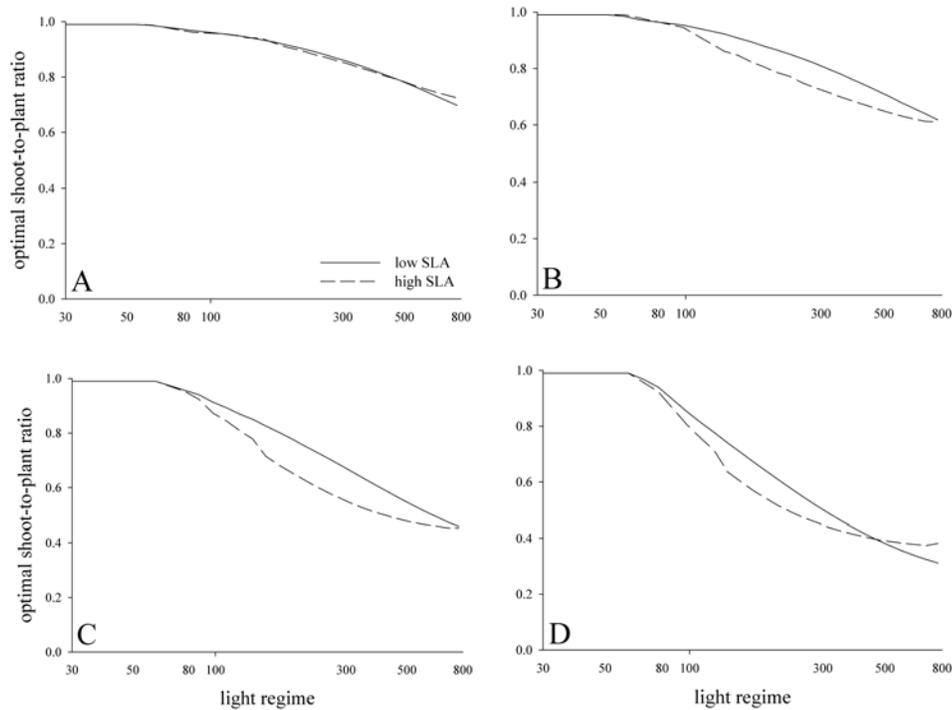


Figure 8 Optimal shoot-to-plant ratio over a range of constant light availabilities for model species with a low SLA (solid line; $\text{SLA} = 0.0025 \text{ m}^2 \text{ g}^{-1}$) and a high SLA (dashed line; $\text{SLA} = 0.015 \text{ m}^2 \text{ g}^{-1}$). A) $n_a = 0.3$, B) $n_a = 0.1$, C) $n_a = 0.03$ and D) $n_a = 0.01$.

growth was slow and, consequently, N demand was low, minimizing the need for root biomass. Consequently, nitrogen availability did not have an effect on σ^* in the low light range. At higher light availability, the effect of nitrogen was as expected. At low N availability, the model selected for a low σ , and σ^* increased with increasing N. A lower SLA, associated with a lower photosynthetic capacity and a smaller light capturing area per gram leaf mass, selected for a higher shoot-to-plant ratio. At low light availability, no effect of SLA was found. Here an increase in the relative amount of aboveground biomass apparently had a larger effect on biomass production than did SLA. At higher light availabilities, the effect of SLA on optimal shoot-to-plant ratio gradually became smaller. This can be attributed to the effect of self-shading. Plant species with a higher SLA will encounter a more severe self-shading, especially at high light availability where growth is fast. Therefore, these species will need more shoot-biomass to fulfil the carbon demands of growth and maintenance.

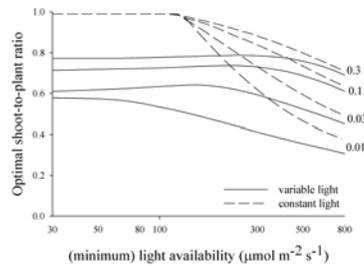


Figure 9 Comparison of the optimal σ of a species with SLA = $0.0025 \text{ m}^2 \text{ g}^{-1}$ at constant (dashed line) and variable (solid line) light regime at different values of nitrogen availability as indicated by the numbers on the right.

The effect of a variable light regime, mimicking a decreasing light availability in the course of the growing season, on optimal shoot-to-plant ratio is illustrated in Figure 9. The variable light regime resulted in a lower optimal shoot-to-plant ratio than a constant light regime. Although carbon was expected to play a determining role in this pattern, Figure 10 shows that internal nitrogen concentration was the factor steering the selection of σ^* . This figure shows the total plant mass (A) and the internal C and N concentrations (B and C) of two species growing at a variable light regime decreasing from 67% to 10% of the light

availability above the forest canopy. The species represented by the filled circles possessed the optimal σ in this light regime. The other species (open circles) had a much higher σ , fit for high biomass production at a constant light intensity of 10%. Initially, the high- σ grew faster (Figure 10A). However, growth of this species slowed down quickly and after approximately 40 days total plant mass did not change any more. The other species started off growing slower but kept increasing in biomass all through the growing season. The leveling off of total plant mass of the high- σ species coincided with the decrease in N concentration in the substrate pool of the plant (Figure 10C). This is due to the high N demand to support the fast initial growth, in combination with the low uptake due to a small root biomass. After approximately 40 days the N concentration reached the minimum concentration required for growth, indicated by the dotted line, and growth stopped completely. The species with a larger amount of its biomass invested in root mass did also experience a steep decrease in N concentration but the concentration remained

well above the minimum for growth. That carbon was not limiting growth, especially not in the high- σ species can be concluded from Figure 10B.

The example taken here shows the effect of nitrogen on the selection of the optimal shoot-to-plant ratio under variable light in the most extreme way. However, even if a shoot-to-plant ratio was taken that is only slightly above the optimal shoot-to-plant ratio, similar results were found (data not shown).

Thus, the optimal σ decreased with increasing light availability and decreasing nitrogen supply. Furthermore, the higher the SLA of the model plant, the lower the optimal σ . A variable light regime resulted in a lower optimal shoot-to-plant ratio compared to a constant light intensity. This resulted from nitrogen limitation of growth at higher shoot-to-plant rather than from carbon limitation.

DISCUSSION

Recently it has been suggested that minimization of biomass loss and maintenance respiration rates, both associated with a low Specific Leaf Area (SLA), play a central role in adaptation to low light conditions, despite the low photosynthetic capacity that is interrelated with these traits (Walters & Reich, 1999). The results of the model simulations presented in this chapter support this hypothesis. Under constant low light conditions the highest biomass was achieved by species with a low SLA, long biomass lifespan and low maintenance respiration rates. If light conditions were less severe the model selected for a higher SLA, associated with a shorter lifespan and higher maintenance costs but also a higher photosynthetic capacity. As already pointed out in the introduction, this topic has not been systematically measured, analyzed and described so data supporting our findings are scarce. Many studies have characterized species from low resource environments, including species indicated as shade tolerant, as slow growers (e.g. Grime & Hunt, 1975;

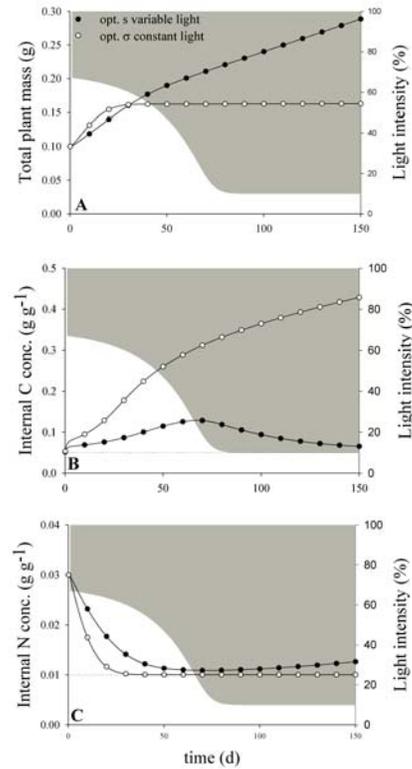


Figure 10 Comparison of (A) the total plant mass, (B) the C concentration in the substrate pool, and (C) the N concentration in the substrate pool at variable light regime (minimum light intensity $120 \mu\text{mol m}^{-2} \text{s}^{-1}$) of a species with the optimal shoot-to-plant ratio in this light regime (filled circles) and a species with the optimal shoot-to-plant ratio found at constant light (light intensity $120 \mu\text{mol m}^{-2} \text{s}^{-1}$; open circles). The shades in the background represent the decrease in light availability during the simulation period, the dotted vertical lines represent the minimum C or N concentration required for growth.

Grubb, 1998; Huante & Rincon, 1998; Lambers & Poorter, 1992; Reich *et al.* 1998b; Walters & Reich, 1996). These species maintain a low Relative Growth Rate (RGR) even when grown under non-limiting growth conditions. In the current methodology for plant growth analysis SLA is used as one of the determinants of RGR (West *et al.*, 1920) and is pointed out as the main factor determining inherent differences in growth rate between herbaceous species (Poorter & Van der Werf, 1998). A high RGR is then associated with high SLA-values while inherently slow-growing species tend to have a lower SLA. This indirectly provides support for the results of the model simulations.

The model can also be used to determine which of the two leaf functional traits associated with the conservation strategy, lifespan and maintenance respiration rate, is the most important factor underlying the selection of a low SLA under low light conditions. The systematic change in those two traits clearly showed that maintenance respiration rate had a larger effect on the selection of the optimal SLA than did longevity. This would suggest that conservation of energy is more important at low light conditions than conservation of existing biomass. However, the systematic variation in the correlated trait relations may not reflect the actual variation in the empirical dataset underlying the trait correlations. Using data on the confidence interval of the plant functional trait datasets in this test might be a valuable contribution.

One of the benefits of the simulation model is that it translates species characteristics on a leaf functional scale to the plant performance on a whole plant scale. Firstly, this is illustrated by the effect of shoot-to-plant ratio on the patterns described for the optimal SLA. At low light conditions, a higher shoot-to-plant ratio enabled the plant to maintain a higher SLA for optimum biomass production. Higher shoot-to-plant mass allowed a higher carbon gain and released the need for conservation. Evaluation of the effect of leaf functional traits on the whole plant level thus modulates general rules that would result from analyses at the leaf level. Furthermore, it illustrates the interaction between different plant traits in the effect on plant performance. Secondly, the value of assessment of the effect of leaf functional traits on the whole plant scale becomes clear from the results found at high light availability. In the model simulations SLA* decreased with increasing light availability and the effect shoot-to-plant ratio had on SLA* reversed for the high- σ species. Both results were attributed to the effect of self-shading. This illustrates that characteristics that bring about an advantage on one scale (the leaf scale) may entail disadvantages on another scale. The plant has several options to cope with the effect of self-shading and optimize performance. As can be concluded from the model simulations, the plant can either decrease its SLA or its shoot-to-plant ratio. These options are not often described in literature. Furthermore, the plant can drop the heavily shaded leaves at the bottom of its canopy more rapidly. This especially occurs in fast-growing plants (Hirose & Werger, 1987; Berntson & Weiner, 1991). Inclusion of such an increased turnover would be a valuable extension of the model. Evaluation of the effect of lower scale mechanisms on the total plant scale processes contributes to the assessment of the role leaf functional trait correlations play in the variation in plant characteristics within and between habitats.

Discussion

The relations between the leaf functional traits used in this model are taken from literature (Reich *et al.* 1992, 1998a, 1998c, but also Ackerly & Reich, 1999; Reich *et al.* 2003; Westoby *et al.* 2000; Wright *et al.*, 2004). The equations are based on statistical fits of the information of a large dataset composed of species from different ecosystems. Although variation is found, the data in literature are constrained within tightly bound domains, and the absence of outliers is striking (Wright *et al.*, 2004). This suggests a role for physiological, physical and morphological causation. Still, the results described above should not be qualitatively determined by parameters of the correlated trait relations. The model simulations in which slopes and intercepts of the correlated traits relations were altered showed that this was not the case; the qualitative pattern did not change. Plant characteristics of the correlated trait scheme are recurrently mentioned as important determinants in shade-tolerance and species-specific adaptation to light conditions in general. The model simulations as presented in this chapter provide a quantitative analysis of the role of those traits.

As the pattern at constant light conditions confirmed the hypothesis, the question was raised what optimal SLA would be simulated under a variable light regime where light availability decreases in the latter part of the growing season, as in a deciduous forest. Application of this variable light regime, mimicking that experienced by the understory of a deciduous forest, selected for a lower optimal SLA than found under constant light conditions equaling the minimum light availability in the variable regime. Mechanisms underlying this pattern were growth limitation and net biomass production. Under the high light conditions in the beginning of the growing season, as plants grew fast, growth of the high-SLA species was stronger limited by nitrogen, due to a high N demand for the production of new biomass, than was the plant with a lower SLA. Carbon availability did not severely limit plant growth. In the low light period, the net biomass production rate of the high-SLA species lagged behind that of the low-SLA species. This could be attributed to the shorter biomass lifespan of the high-SLA species and the low production of biomass due to the high maintenance respiration and the low light intensity. Apparently, the higher light availability at the beginning of the growing season did not release the need for conservation of biomass and energy; production of a large biomass with a high N demand, short lifespan and high maintenance costs had a negative impact on net biomass production of the high-SLA plant over the larger part of the growing season. Not many studies describing plant growth responses to a change in light intensity from high to low intensity are available, nor studies comparing species from the understories of evergreen and deciduous forests. An effect of low nutrient availability on growth of species in the high-light period has been described for *Geum urbanum* and *Cirsium palustre* as well as for some tropical crops (Pons, 1977). Pons (1977) also found that the RGR of a shade-tolerant and a shade-intolerant species transferred from full daylight to 4.6% daylight declined immediately after the transfer to a level lower than for control plants grown at that intensity. This suggests that the larger plant size, and thus a larger maintenance respiration, at the time of transfer played a role in the determination of the

RGR. No difference, however, was found between *Geum* and *Cirsium*. This can be due to only a small difference in respiration rate between the two species. Furthermore, the species differed in the extent to which they could adjust their morphology and physiology to the new low-light conditions in order to compensate for the reduced growth as a consequence of the change in light availability (Pons, 1977).

Morphological and physiological acclimation to changed (light) conditions is a widely described phenomenon in plants. It is commonly assumed that fast-growing species are better capable of adjusting to the new environment than are slow-growing species. Morphological adjustment to a variable light climate are further studied in the next chapter.

The between-species pattern in adaptation of shoot-to-plant ratio to different growing environments followed, as expected, the pattern described for the plastic acclimation of plants to changes in their growing environments. The optimal shoot-to-plant ratio in a variable light regime, mimicking the light availability under a deciduous forest canopy, was reduced compared to the shoot-to-plant ratio found at a constant availability of the light intensity in the shaded period of the growing season. The driving force behind this selection for a lower shoot-to-plant ratio was nitrogen limitation. Due to the fast growth in the initial high-light period, species with a high shoot-to-plant ratio encountered a shortage of N to support the fast growth. However, the nitrogen availability is not constant during the year. In the spring, as the soil warms up a flush of nitrogen temporarily increases N availability. The spring-time nitrogen availability model simulations may thus be underestimated. Still, in nutrient-poor systems, nitrogen availability will be in low supply in the rest of the growing season and severely limit growth of species possessing a high shoot-to-plant ratio.

When interpreting the simulation results one should bear in mind that the model species is defined as an annual species aimed at maximizing its net biomass production over the growing season. The results of the simulations studying the effect of shoot-to-plant ratio in a deciduous light regime (Figure 12) showed that a species with a high shoot-to-plant ratio was able to realize a fast growth in the initial high light period, in the low light period later in the season, when growth had stopped due to nitrogen limitation internal carbon concentrations increased. For a perennial species in the forest understory it thus may be profitable not to invest too strongly in belowground resource acquiring tissue (fine roots).

APPENDIX I: ANALYTIC MODEL

MODEL DESCRIPTION

An analytic model can be used to analyze the steady-state situation of a system. It is a static model, assuming all variables and parameters to be independent of time. To increase the understanding and underpinning of the patterns found in the simulation model, the effect of Specific Leaf Area (SLA in $\text{m}^2 \text{g}^{-1}$) on the biomass production of a plant can be studied in an analytic model.

The biomass production, in this model analyzed as the relative growth rate (RGR), results from the relative biomass production rate (μ , in $\text{g g}^{-1} \text{d}^{-1}$) minus the biomass turnover rate (τ , in $\text{g g}^{-1} \text{d}^{-1}$):

$$\frac{d_m/d_t}{m} = \mu - \tau \quad (\text{I.1})$$

Where d_m/d_t is the growth rate of the plant in g d^{-1} and m is the plant mass in g . Since μ and τ are both functions of SLA, relative growth rate also is a function of SLA.

The relation between τ and SLA is identical to the exponential decay relation used in the simulation model, which is described in Chapter 2 (equations 19 to 21). With $b_L > 1$, this resulted in a concave upward τ with increasing SLA.

$$\tau = \ln(k) \cdot a_L \cdot SLA^{b_L} \quad (\text{I.2})$$

The turnover of above and belowground biomass is assumed to be equal and both are related to SLA.

The relation between μ and SLA is more complex and cannot be explained in one equation. First, μ is determined by the net carbon gain rate (in $\text{g C g}^{-1} \text{d}^{-1}$) divided by the carbon costs of the production of new biomass (in $\text{g C g}^{-1} \text{d}^{-1}$), i.e.

$$\mu = \frac{(\sigma \cdot P_g - R_m)}{c_{si}} \quad (\text{I.3})$$

Where σ is the shoot-to-plant ratio, P_g is the gross carbon gain rate per unit shoot mass in $\text{g C g}^{-1} \text{d}^{-1}$, R_m is the maintenance respiration rate per unit plant mass in $\text{g C g}^{-1} \text{d}^{-1}$ and c_{si} is the carbon construction cost for new biomass (including growth respiration) in g C g^{-1} . Both P_g and R_m are variable and change with SLA. Shoot-to-plant ratio and the construction cost of new biomass are assumed to be constants. In this model we assume

that the aboveground mass only consists of leaf biomass and, similarly, belowground mass only consists of fine root mass. Like in the simulation model, no distinction is made between the maintenance respiration of above- and belowground biomass.

In the simulation model the photosynthetic capacity per unit leaf mass P_{gm} is indirectly, via mass-based leaf nitrogen concentration $[N]$, correlated to SLA:

$$[N] = a_n + b_n SLA \quad (I.4)$$

This is then used to describe a direct P_{gm} -SLA relation, based on the correlations used in the simulation model:

$$P_{gm} = a_p + b_p [N] = a_p + b_p (a_n + b_n SLA) \quad (I.5a)$$

Hence:

$$P_{gm} = a'_p + b'_p SLA \quad (I.5b)$$

with:

$$a'_p = a_p + b_p a_n$$

$$b'_p = b_p b_n$$

The parameters a_p , b_p , a_n and b_n are taken from the relations represented in Table II in the main text.

The actual photosynthetic rate per unit leaf-area, P_{gL} in $\text{g C m}^{-2} \text{s}^{-1}$, is calculated using a rectangular light-response curve. In the simulation model the more realistic non-rectangular hyperbola is used. Since the analytic model is exclusively used to study the pattern of the optimal SLA in relation to light availability and σ , and the choice of photosynthesis-light relation does not affect those patterns, here the simpler form is used:

$$P_{gL} = \frac{P_{gmL} \cdot \Phi \cdot i_L}{P_{gmL} + \Phi \cdot i_L} \quad (I.6)$$

where Φ is the quantum yield ($\mu\text{mol CO}_2 \mu\text{mol photons}^{-1}$), i_L the light intensity per unit leaf area (in $\mu\text{mol m}^{-2} \text{s}^{-1}$) and, P_{gmL} the photosynthetic capacity per unit leaf area (in $\text{g C m}^{-2} \text{s}^{-1}$). P_{gmL} can be derived from P_{gm} and SLA:

$$P_{gmL} = \frac{P_{gm}}{SLA} \quad (I.7)$$

Appendix

And similarly i_L can be described as a function of SLA and i , the light availability per unit leaf mass,

$$i_L = \frac{i}{SLA} \quad (I.8)$$

P_g can then be calculated by multiplying the actual area-based photosynthetic rate P_{gL} with the specific leaf area,

$$P_g = P_{gL} \cdot SLA \quad (I.9)$$

The R_m -SLA relation can be described as a simple linear relation, resulting from reformulating the above described P_{gm} -SLA relation (Equation I.5) and the R_m - P_{gm} relation described in Table II of the main text.

$$R_m = a_r + b_r P_{gm} = a_r + b_r (a'_p + b'_p SLA) \quad (I.10a)$$

Thus: (I.10b)

$$R_m = a'_r + b'_r SLA$$

with:

$$a'_r = a_r + b_r a'_p$$

$$b'_r = b_r b'_p$$

Now, the components of the relative growth rate are all defined as constants or functions of SLA. This set of equation can thus be used to study the optimal SLA and the response to light intensity and shoot-to-plant ratio. P_g , the gross photosynthetic rate, is also a function of light availability.

REWRITING THE PHOTOSYNTHESIS-LIGHT RELATION

The photosynthesis-light relation clearly is the most complex component of the calculation of the RGR. To facilitate further analysis, a simplification of Equation I.6 is required. First, two new dimensionless variables, ξ and $\psi(\xi)$, are introduced,

$$\xi = \frac{\Phi \cdot i_L}{P_{gmL}} \quad (I.11)$$

and:

$$\psi(\xi) = \frac{\xi}{1 + \xi} \quad (I.12)$$

Then the photosynthesis-light relation can be rewritten to:

$$P_{gL} = P_{gmL} \cdot \frac{(\Phi \cdot i_L / P_{gmL})}{1 + (\Phi \cdot i_L / P_{gmL})} = P_{gmL} \cdot \frac{\xi}{1 + \xi} = P_{gmL} \cdot \psi(\xi) \quad (I.13)$$

As is shown in Figure 1 the function $\psi(\xi)$ is concave upward in ξ between 0 and 1. This leads to the following pattern, when $\xi=0$, $\psi(\xi)=0$ and thus, $P_{gL}=0$, while when ξ goes to large values, $\psi(\xi)$ goes to 1 and P_{gL} goes to P_{gmL} . Since Φ is assumed to be constant, the value of ξ changes with i_L or with P_{gmL} .

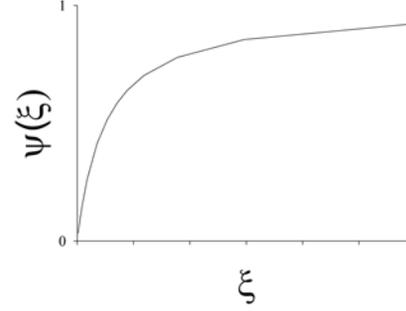


Figure 1 The relation between ξ and $\psi(\xi)$.

The description of the photosynthesis-light relation uses the area-based photosynthesis. In the calculation of the relative growth rate (Equation I.3) however, the mass-based photosynthesis is used. Since both i_L and P_{gmL} can be described as functions of SLA (Equation I.7 and I.8) the mass-based and area-based photosynthesis can be treated as equal, i.e.

$$\xi = \frac{\Phi \cdot i_L}{P_{gmL}} = \frac{\Phi \cdot (i/SLA)}{(P_{gm}/SLA)} = \frac{\Phi \cdot i}{P_{gm}} = \xi \quad (I.14)$$

In other words, the carbon gain rate per unit leaf mass P_g , has exactly the same form in terms of i and P_{gm} , the mass-based photon absorption rate and photosynthetic capacity respectively, as P_{gL} , the carbon gain rate per unit leaf area, has in terms of the area-based photon absorption rate and photosynthetic capacity, i_L and P_{gmL} respectively.

$$P_g = \psi(\xi) \cdot P_{gm} \quad (I.15)$$

For further analysis, the expression of ξ as function of SLA is also required. So, Equation I.11 can be expanded with:

$$\xi = \frac{\Phi \cdot i_L}{P_{gmL}} = \Phi \cdot i_L \cdot \frac{S_{LA}}{P_{gm}} \quad (I.16)$$

The above equations can be used to study the effect of light on the optimal SLA.

EFFECT OF LIGHT ON THE OPTIMAL SLA

In this analytic model, optimal SLA is defined as the SLA at which relative growth rate is maximized, i.e. the SLA at which the difference between biomass production rate and turnover rate is largest. Since gross photosynthetic rate is affected by the light intensity, this factor is also expected to influence the growth rate of the plant, and thus the value of the optimal SLA. To evaluate the effect of SLA on the relative growth rate the following equation is used:

$$G(i_L, SLA) = \frac{\sigma \cdot P_g(i_L, SLA) - R_m(SLA)}{c_c} - \tau(SLA) \quad (I.17)$$

The optimal SLA, from now on referred to as SLA^* , is found by solving the derivative of this function to SLA

$$G(i_L, SLA^*) = \frac{\sigma \cdot \frac{\partial}{\partial S} P_g(i_L, SLA^*) - \frac{\partial}{\partial S} R_m(SLA^*)}{c_c} - \frac{\partial}{\partial S} \tau(SLA^*) = 0 \quad (I.18)$$

To determine the response of the SLA^* to a change in the light intensity, the implicit function theorem is applied, resulting in:

$$\frac{dSLA^*(i_L)}{di_L} = - \frac{\frac{\partial}{\partial i_L} G(i_L, SLA^*(i_L))}{\frac{\partial}{\partial S} G(i_L, SLA^*(i_L))} \quad (I.19)$$

with:

$$\frac{\partial}{\partial i_L} G(i_L, SLA^*(i_L)) = \frac{\sigma \frac{\partial^2}{\partial i_L \partial S} P_g(i_L, SLA) - \frac{\partial^2}{\partial i_L \partial S} R_m(SLA)}{c_c} - \frac{\partial^2}{\partial i_L \partial S} \tau(SLA)$$

and:

$$\frac{\partial}{\partial_s} G(i_L, SLA^*(i_L)) = \frac{\partial}{\partial_s} \left(\frac{\sigma \frac{\partial}{\partial_s} P_g(i_L, SLA) - \frac{\partial}{\partial_s} R_m(SLA)}{c_c} - \frac{\partial}{\partial_s} \tau(SLA) \right)$$

The shoot-to-plant ratio σ and carbon investment in new biomass c_{si} are assumed to be constant. The functions $\partial/\partial_s R_m(SLA)$ and $\partial/\partial_s \tau(SLA)$ are not a function of light intensity, so differentiation of these functions to i_L returns the value zero. Furthermore, the relation between maintenance respiration R_m and SLA is described by a linear function, which leads to $\partial^2_{SLA} R_m = 0$. Thus, Equation I.19 can be rewritten as:

$$\frac{dSLA(i_L)}{di_L} = \frac{\left(\frac{\sigma \frac{\partial^2}{\partial i_L \partial_s} P_g(i_L, SLA)}{c_c} \right)}{\left(\frac{\sigma \frac{\partial^2}{\partial_s^2} P_g(i_L, SLA)}{c_c} \right) - \frac{\partial^2}{\partial_s^2} \tau(SLA)} \quad (I.20)$$

If the above equation results in a positive sign, light intensity is positively correlated to SLA^* , if a negative result is found, light intensity has a negative effect on SLA^* . Due to the complexity of the equation the sign of the numerator $\partial/\partial i_L G(i_L, SLA^*(i_L))$ and denominator $\partial/\partial_s G(i_L, SLA^*(i_L))$ will be studied separately.

First the denominator will be examined more closely. As is described in Equation I.2 τ is a concave upward function in SLA. Therefore, the second order derivative $\partial/\partial_s^2 \tau(SLA)$ is positive but results in a negative value due to the preceding negative sign of the term. The first term of the denominator, or more specifically, second order derivative $\partial/\partial_s^2 P_g$ needs some more attention:

$$\frac{\partial}{\partial_s^2} P_g = \frac{\partial}{\partial_s} \left[\frac{\partial}{\partial_s} P_g \right] \quad (I.21)$$

In Equation I.15 P_g is defined as function of $\psi(\xi)$ and P_{gm} , thus the effect of SLA on P_g , the first order derivative of P_{gm} to SLA, can be described as follows:

Appendix

$$\begin{aligned}
 \frac{\partial}{\partial s} P_g &= \frac{\partial}{\partial s} [\psi(\xi) \cdot P_{gm}] = \frac{\partial}{\partial s} (\psi(\xi)) \cdot P_{gm} + \psi(\xi) \cdot \frac{\partial}{\partial s} (P_{gm}) \\
 &= \frac{d\psi(\xi)}{d\xi} \cdot \Phi \cdot \left(\frac{d(i_L \cdot P_{gm})}{ds} - i_L \cdot \frac{dP_{gm}}{ds} \right) \cdot P_{gm} + \psi(\xi) \cdot \frac{dP_{gm}}{ds} \\
 &= \frac{d\psi(\xi)}{d\xi} \cdot (\Phi \cdot i_L) + \left(\psi(\xi) - \xi \cdot \frac{d\psi(\xi)}{d\xi} \right) \cdot a'_p
 \end{aligned} \tag{I.22}$$

This equation can then be substituted into Equation I.21 and subsequently the second order derivative can be determined.

$$\begin{aligned}
 \frac{\partial}{\partial s} \left[\frac{\partial}{\partial s} P_g \right] &= \frac{\partial}{\partial s} \left[\frac{d\psi(\xi)}{d\xi} \cdot \Phi \cdot i_L + a'_p \cdot \left(\psi(\xi) - \xi \cdot \frac{d\psi(\xi)}{d\xi} \right) \right] \\
 &= \frac{d^2\psi(\xi)}{d\xi^2} \cdot \frac{d\xi}{ds} \cdot \Phi \cdot i_L + a'_p \left(\frac{d\psi(\xi)}{d\xi} \cdot \frac{d\xi}{ds} - \frac{d\xi}{ds} \cdot \frac{d\psi(\xi)}{d\xi} - \xi \cdot \frac{d^2\psi(\xi)}{d\xi^2} \cdot \frac{d\xi}{ds} \right) \\
 &= \frac{d^2\psi(\xi)}{d\xi^2} \cdot \frac{d\xi}{ds} \cdot (\Phi \cdot i_L - a'_p \cdot \xi)
 \end{aligned} \tag{I.23}$$

Using the definition of ξ given in Equation I.16 and the P_{gm} -SLA relation described in Equation I.5, the derivative $d\xi/ds$ can be written as:

$$\frac{d\xi}{ds} = \frac{\Phi \cdot i_L}{P_{gm}^2} \cdot (P_{gm} - SLA \cdot a'_p) = \xi \cdot \left(1 - \frac{a'_p \cdot SLA}{P_{gm}} \right) \tag{I.24}$$

and the last term of Equation I.23 becomes:

$$\Phi \cdot i_L - a'_p \cdot \xi = \Phi \cdot i_L - a'_p \cdot \frac{\Phi \cdot i_L}{P_{gmL}} = \Phi \cdot i_L \cdot \left(1 - \frac{a'_p \cdot SLA}{P_{gm}} \right) \tag{I.25}$$

Substitution of Equation I.24 and I.25 in the definition of the second order derivative of P_g to SLA presented in Equation I.21 simplifies the calculation of $\partial/\partial s^2 P_g$ further to:

$$\frac{d^2 P_g}{ds} = \frac{d^2 \psi(\xi)}{d\xi} \cdot \frac{d\xi}{ds} \cdot (\Phi \cdot i_L - a'_p \cdot \xi) = \frac{d^2 \psi(\xi)}{d\xi} \cdot \xi \cdot \left(1 - \frac{a'_p SLA}{P_{gm}}\right)^2 \quad (I.26)$$

Now it is possible to analyze the sign of the second order derivative $\partial^2/\partial s^2 P_g$. Since a quadratic term always returns a positive value and ξ by definition is positive, the sign of $d^2 P_g/ds$ is determined by the sign of the second order derivative $\partial^2/\partial \xi^2 \psi(\xi)$. The solution can be read from Figure 1. Since $\psi(\xi)$ is a concave downward function of ξ , the second order derivative is negative. Consequently, $\partial^2/\partial s^2 P_g$ is also negative.

So, because both terms are negative, the denominator of Equation I.20 has a negative value. Next step is to study the sign of the numerator $\partial/\partial i_L G(i_L, SLA^*(i_L))$. Since σ and c_c are constant, the sign of the numerator is determined by the sign of the term $\partial^2/\partial i_L \partial s P_g(i_L, SLA)$. The derivative $\partial/\partial s P_g$ is already analyzed in Equation I.22 and can easily be substituted.

$$\frac{\partial}{\partial i_L \partial s} P_g = \frac{\partial}{\partial i_L} \left[\frac{d\psi(\xi)}{d\xi} \cdot \Phi \cdot i_L - a'_p \cdot \left(\psi(\xi) - \xi \cdot \frac{d\psi(\xi)}{d\xi} \right) \right] \quad (I.27)$$

Differentiation to i_L then gives:

$$= \frac{d^2 \psi(\xi)}{d\xi} \cdot \frac{d\xi}{di_L} \cdot \Phi \cdot i_L - \frac{d\psi(\xi)}{d\xi} \cdot \Phi - a'_p \cdot \xi \cdot \frac{d^2 \psi(\xi)}{d\xi} \cdot \frac{d\xi}{di_L} \quad (I.27a)$$

This equation can be simplified by solving the term $d\xi/di_L$.

$$\frac{d\xi}{di_L} = \frac{d\left(\frac{\Phi \cdot i_L}{P_{gmL}}\right)}{di_L} = \frac{\Phi}{P_{gmL}} \quad (I.28)$$

And:

$$\frac{d\xi}{di_L} \cdot \Phi \cdot i_L = \frac{\Phi}{P_{gmL}} \cdot \Phi \cdot i_L = \Phi \cdot \xi \quad (I.29)$$

So, Equation I.27a, the numerator $\partial_{i_L} G(i_L, SLA^*(i_L))$, can be further simplified to:

Appendix

$$\frac{\partial^2}{\partial_{iL}\partial_S} P_g = \Phi \cdot \xi \cdot \frac{d^2\psi(\xi)}{d\xi^2} \cdot \left(1 - \frac{a'_p}{P_{gmL}}\right) + \frac{d\psi(\xi)}{d\xi} \cdot \Phi \quad (I.30)$$

Finally, Equation I.5 and I.7 can then be used to simplify the term $1 - a'_p/P_{gmL}$, which leads to:

$$1 - \frac{a'_p}{P_{gmL}} = 1 - \frac{a'_p \cdot S_{LA}}{a'_p \cdot S_{LA} + b'_p} = \frac{b'_p}{a'_p \cdot S_{LA} + b'_p} = \frac{b'_p}{P_{gm}} \quad (I.31)$$

and consequently, substitution of Equation I.31 into Equation I.30 results in:

$$\frac{\partial^2}{\partial_{iL}\partial_S} P_g = \Phi \cdot \left(\frac{b'_p}{P_{gm}} \cdot \xi \cdot \frac{d^2\psi(\xi)}{d\xi^2} + \frac{d\psi(\xi)}{d\xi} \right) \quad (I.32)$$

To analyse the sign of this derivative the first and second order derivatives $d\psi(\xi)/d\xi$ and $d^2\psi(\xi)/d\xi^2$ have to be explicitly defined in terms of ξ .

$$\frac{d\psi(\xi)}{d\xi} = \frac{1}{(1+\xi)^2} \quad (I.33)$$

and:

$$\frac{d^2\psi(\xi)}{d\xi^2} = \frac{-2}{(1+\xi)^3} \quad (I.34)$$

Substitution of these two equations into Equation I.32 results in:

$$\frac{\partial^2}{\partial_{iL}\partial_S} P_g = \Phi \cdot \frac{1}{(1+\xi)^2} \cdot \left(1 - \frac{b'_p}{a'_p \cdot S_{LA} + b'_p} \cdot \frac{2\xi}{(1+\xi)}\right) \quad (I.35)$$

Since Φ and the term $1/(1+\xi)^2$ always result in a positive value, the sign of this derivative depend on the value of the second term between the parenthesis. If this term is smaller than one, the equation, and thus the numerator, results in a positive value. If this term is larger than one, the derivative is negative.

The value of the term $2\xi/(1+\xi)$ lies between zero and two, so the complete term lies between zero and $2b'_p/(a'_p \cdot S_{LA} + b'_p)$. If b'_p would be large compared to a'_p , then the term would result in a value larger than one. However, in Table II b'_p is defined to be

appreciably smaller than a_p' and a_p' SLA is always larger than b_p' so this term always has a value smaller than 1. This result, as already explained above, in a positive value for the numerator.

So, now the sign of the denominator (negative) and the numerator (positive) of Equation I.19 is analysed the response of the SLA* to a change in light intensity is determined to be positive. This implies that the optimal SLA increases with increasing light intensity.

EFFECT OF SHOOT-TO-PLANT RATIO ON THE OPTIMAL SLA

To find the response of SLA* to a change in the shoot-to-plant ratio σ the effect of SLA on RGR and the effect of σ on RGR has to be analyzed. The implicit function theorem leads to:

$$\frac{dSLA}{d\sigma} = - \frac{\frac{\partial}{\partial \sigma} RGR}{\frac{\partial}{\partial s} RGR} \quad (I.36)$$

The derivative ∂/∂_s RGR corresponds to the denominator of Equation I.19, which is analyzed to be negative in the previous section.

Differentiation of RGR to σ results in:

$$\frac{\partial}{\partial \sigma} RGR = \frac{\partial}{\partial \sigma} \left(\frac{\sigma \frac{\partial}{\partial s} P_g(SLA) - \frac{\partial}{\partial s} R_m(SLA)}{c_c} - \frac{\partial}{\partial s} \tau(SLA) \right) \quad (I.37)$$

The derivative $\partial/\partial_s P_g(SLA)$ is analyzed in Equation I.22. The definition of $d\psi(\xi)/d\xi$ in Equation 33 shows this derivative always is positive. Since all other variables in Equation I.22 also have positive values, $\partial/\partial_s P_g(SLA)$ is positive. Consequently, shoot-to-plant ratio has a positive effect on SLA*.

VALUE AND LIMITATION OF A SIMPLE ANALYTIC MODEL

The simplification of the system applied in this analytic model enhances understanding of a complex system and enables analyses of a part of the system. This consolidates the results of the simulation model and contributes to the underpinning of the conclusions.

Appendix

However, because important processes as overshadowing and processes of the nitrogen economy are missing, the analytic model proves to be unfit to analyze the total problem of a growing plant.

Chapter 4

The role of plasticity in shoot-to-plant ratio under different light and nitrogen conditions

ABSTRACT

Plasticity in biomass allocation is generally believed to be adaptive. A number of environmental factors have been suggested to operate in the selection for plasticity, e.g. temporal heterogeneity in the environment and mean resource availability. Furthermore, it has also been hypothesized that certain species traits, for instance inherent growth rate, are related to plasticity. In this study the question was addressed whether or not plasticity is advantageous in the large temporal heterogeneity in light availability, in combination with different levels of nitrogen supply, in the understory of deciduous forests. In addition, it was tested if species differing in inherent growth rate should react differently. To answer these questions, a modeling approach was followed. The simulation results showed that functional plasticity is unfavorable if the main direction of allocation (to above- or belowground biomass) in the high-light phase of the growing season is opposite to that later in the season. If growth was limited the most by the same resource all through the season, functional plasticity showed to be advantageous. Fast-growing species and environments supporting fast growth required a lower functional plasticity since fast growth enabled a fast adjustment of shoot-to-plant ratio even if functional plasticity level was low.

From the simulations it can be concluded that for understory species of dense forest and low nutrient supply should a rigid allocation strategy is more favorable.

Keywords: biomass allocation, deciduous forest understory, light, inherent growth rate, mechanistic plant growth model, nitrogen supply, plasticity.

INTRODUCTION

Plasticity in biomass allocation is generally believed to be adaptive (Steinger *et al.*, 2003; Glynn *et al.*, 2003). Plasticity is adaptive when it allows a species to maintain fitness under diverse environmental conditions (Sultan & Spencer, 2003). High plasticity then increases tolerance to environmental variation and leads to a higher fitness compared to that of a rigid plant. Still, large differences in plasticity are found between species. This could be because plasticity is advantageous under some conditions but not under others (Schaffer *et al.*, 1982).

Because this study addresses the adaptation of plants to light and nitrogen availability, the focus is on plasticity in biomass allocation to light and nitrogen acquiring biomass. A number of environmental factors have been suggested to operate in the selection for plasticity, one of which being temporal heterogeneity in the environment. Whether temporal heterogeneity in the environment will select for plasticity in a trait should depend upon the match between the duration of the environmental states and the response time of the trait. If the temporal scale of heterogeneity in the environment is either too small or too large for the response time of the trait, no plastic response to heterogeneity is to be expected (Alpert & Simms, 2002; Stuefer, 1996).

An environmental factor that is often mentioned in relation to spatial heterogeneity is contrast between different states (Stuefer, 1996). This factor may also affect the selection for plasticity in relation to temporal heterogeneity. If contrast between two environmental states is small, the plant will only have to make small adjustments and temporal heterogeneity is not expected to be of large importance in selection of plasticity. A high contrast would require much larger adjustments that may not be within the potency of the species to fulfil. In this last case, a rigid strategy, adapted to either one of the environmental states encountered, or to some mean level of resource availability, may be more profitable. Between these two extremes, contrast between environmental states is expected to select for plasticity.

Another environmental factor that has been brought forward as playing a role in selection for plasticity is the mean resource availability in the environment (Alpert & Simms, 2002). Plasticity has been hypothesized to be more advantageous in habitats where resource availability is higher overall (Alpert & Simms, 2002). Plants are likely to grow faster when resources are more abundant (Chapin, 1980). This should reduce the time required for many responses and benefits may outweigh costs fast. Consequently, it has been hypothesized that species from more extreme habitats may be less plastic (Alpert & Simms, 2002; Grime & Mackey, 2002). This has been attributed to the costs of plasticity that, under low resource availability, may not be offset by the advantages of plasticity. Costs may be involved in maintenance and production of the sensory mechanisms, plasticity genes, developmental instability, information acquisition and assessment of the environment (DeWitt *et al.*, 1998). Furthermore, plasticity in morphological plant traits, like shoot-to-plant ratio, involves the costs of production, shedding and replacement of

Introduction

plant parts with different characteristics (Grime & Mackey, 2002) and, to a certain extent, the plant has to deal with the consequences of past investments.

Besides environmental factors, it has also been hypothesized that certain species traits are related to plasticity, for instance species inherent growth rate, affecting the time it takes to respond to changes in the environment (Alpert & Simms, 2002). A high inherent species growth rate would then be connected to high plasticity while slow-growing species should be more rigid.

In the understory of a deciduous forest the availability of light, one of the main resources for growth, exhibits large temporal variation over the growing season. In the beginning light availability is high, while later in the season light availability decreases rapidly and drastically (Anderson, 1964; Kato & Komiyama, 2002; Pons, 1976). The duration of the environmental states in relation to the length of the growing season of many species should give species sufficient time to adjust to the new situation and profit from that. In this situation, selection for plasticity would be expected. However, depending on the type of forest and the tree species that forms the canopy layer, differences between the high and the low light phase can be high, and thus would plead for selection of low plasticity or a rigid strategy. This leads to the question whether or not plasticity is advantageous for plants adapted to the understory of deciduous forests.

Besides the availability of light, the availability of nitrogen in the soil also plays a role in the plastic response of biomass allocation. In many soils of natural or nearly natural temperate forests the N supply to the vegetation is deficient (Falkengren-Grerup *et al.*, 1998; Runge, 1971). During the growing season there generally is a continuous availability of nitrogen for plant growth (DeWilligen & VanNoordwijk, 1987). Although the temporal variation is low, in combination with the temporally varying light intensity, the availability of nitrogen relative to the availability of light will vary in the course of the season and may therefore play a part in the adjustment of the plant to its growth environment and the selection of plasticity.

There is little empirical support for a relationship between resource levels, heterogeneity, predictability and plasticity (Alpert & Simms, 2002), and in existing studies forest species were not often included. This can, in part, be attributed to difficulties with defining and measuring plasticity. In different studies different definitions are used and often not plasticity in itself is measured but the outcome of the plastic response. Another problem for experimental studies is that species often differ in more traits than the plastic trait of interest which complicates the interpretation of the results.

A modelling approach, as applied in this study, gives the opportunity to use a strict definition of plasticity, characterize a model species by its potential inherent plasticity which needs not be derived from its response to certain treatments or environments, focus on this one specific trait, and define a series of model species that differ in this trait only. This study addresses plasticity in biomass allocation and in the resulting shoot-to-plant ratio. In the model, plasticity is defined as the growth rate of the aboveground biomass

relative to the growth rate of the belowground biomass. Division of new biomass between shoot and root is steered by the ratio between the internal carbon and nitrogen concentration, which represents the result of processes resource acquisition and use. The model is used to analyze the role of plasticity in plant growth and determine the optimal plasticity level under different conditions. It has a simplified but realistic resource acquisition unit, both for carbon and nitrogen, and includes processes of self-shading and soil nitrogen depletion which leads to decreasing mass-based uptake rates with increasing biomass. Consequently, the model does not assume exponential growth and is therefore not restricted to analysis of the earliest part of the growing season. A detailed description of the model is given in Chapter 2.

METHODS

MODEL DESCRIPTION

To study the role of plasticity in the growth of the plant under different environmental conditions the mechanistic plant model described in Chapter 2 was used. The model plant grows on carbon (C, carbohydrates) and nitrogen (N, amino-acids) and consists of an aboveground and a belowground compartment involved in the uptake of carbon and nitrogen, respectively. The model explicitly considers light extinction within the canopy of the plant. Therefore, light availability in the lower layers of the plant's canopy decreases with the leaf area of the plant, and gross photosynthetic rate per gram leaf consequently goes down. Similarly, with increasing root biomass, N availability in the depletion zone decreases and N uptake rate per gram fine root decreases as well. Acquired C and N are first put into an internal substrate pool from where these resources are used to produce new biomass and cover maintenance respiration demands. Production of one gram of new biomass demands a fixed amount of C and N. The concentrations in the substrate pool determine the amount of new biomass that

Table I List of standard parameter settings and literature sources.

Abbreviation		Value	Unit
r_{nu}	*	0.00125	$g\ g^{-1}\ d^{-1}$
c_c	*	0.8	$g\ g^{-1}$
n_r	¹	0.014	$g\ g^{-1}$
k_c	*	0.2	
k_n	*	0.05	
c_{min}	*	0.05	$g\ g^{-1}$
n_{min}	*	0.01	$g\ g^{-1}$
c_{leth}	*	0.001	$g\ g^{-1}$
n_{leth}	*	0.001	$g\ g^{-1}$
k	*	0.02	-
r_{ac}, r_{bc}	*	0.075	m
ρ_{MaL}, ρ_{MbR}	*	3000	$g\ m^{-3}$
k_H	*	0.25	-
β	*	1.279	-
a_L	²	0.82	-
α_L	³	20	rad
Φ	⁴	0.05	$\mu mol\ \mu mol^{-1}$
θ	⁴	0.8	-
R_{nc}, R_{nd}	*	0.1	$d\ m^{-1}$
k_{nd}	*	0.0714	-
p	*	1	-
p_n	*	5	-

* estimated

** mathematical parameter

¹ Aerts (1996)

² Rosati et al. (2001)

³ Schieving (1998)

⁴ Anten (1995)

can be produced, or in other words, the growth rate. This is determined by a bivariate Michaelis-Menten equation. In principle, the bivariate Michaelis-Menten equation can be seen as the product of two substrate availability factors, one for C and one for N (see Chapter 2).

Substrate av. factor $f(c,n)$ = carbon availability factor . nitrogen availability factor

$$f(c,n) = \frac{(c - c_{\min})}{k_c + (c - c_{\min})} \cdot \frac{(n - n_{\min})}{k_n + (n - n_{\min})}$$

If both resources are in ample supply growth is fast; if the concentration of either one or both resources is low growth is slowed down. Because carbon demand of growth is higher than nitrogen demand, C is limiting growth at higher concentrations than N. If the carbon (or nitrogen) availability factor equals one, carbon (or nitrogen) does not affect growth

rate; if it equals zero, the availability of carbon (or nitrogen) is so low it causes growth to stop. Total plant growth rate is determined by multiplication of the two substrate availability factors (Figure 1).

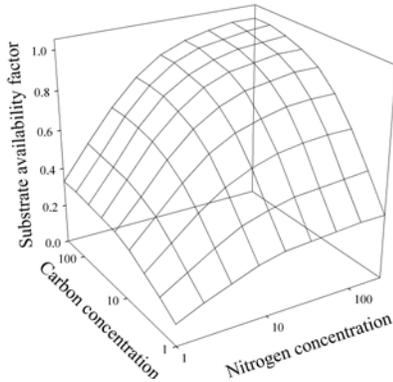


Figure 1 Visualization of the effect of resource supply in the substrate pool on the plant growth rate. The fraction of the growth capacity that can be realized, $f(c,n)$ is presented on the z-axis as function of the carbon and nitrogen concentrations presented on the other two axes.

While the growth rate is determined by the concentrations of C and N, the ratio between N and C concentrations in the substrate pool determines the division of new growth between above and belowground biomass. If the C concentration in the substrate pool is low compared to the N concentration more biomass will be allocated towards the shoot, while a relatively low N concentration will lead to an increased growth of the belowground compartment.

The mechanism that determines the division between above and belowground growth in the model plant is visually represented in Figure 2.

On the x-axis the n/c ratio in the substrate pool is shown, on the y-axis ϕ , the ratio between aboveground growth rate and belowground growth rate.

Allocation ratio I $\phi = \frac{\mu_a^{cap}}{\mu_b^{cap}}$

If ϕ equals one, growth rates of the two compartments is equal, if ϕ is larger than one growth of the aboveground compartment is increased at the cost of the growth of the belowground compartment and if ϕ is smaller than one the opposite is the case.

The plasticity level is defined as the maximum value of ϕ . So, the plasticity level represents the maximum growth rate of the shoot relative to the growth rate of the root. It is calculated as follows:

$$\text{Allocation ratio II} \quad \phi = \text{Max} \tanh\left(\frac{\log v_r}{\alpha}\right)$$

As is explained in Chapter 2 (Equation 12), the above function produces values between $1/\text{Max}$ and Max . If the value of Max is set to one, the allocation control parameter is constant and the aboveground growth capacity equals the belowground growth capacity, resulting in a rigid plant. In this chapter the other parameters that shape the allocation curve, v_{ref} and α , are set to a constant value. Parameter values are given in Table I. The only costs of plasticity that are considered in the model are the consequences of past allocation patterns for the total respiration load of the plant.

SELECTING THE OPTIMAL PLASTICITY LEVEL

The total plant mass at the end of the simulation period of 150 days is used as a measure of plant performance. Different species were defined by a different plasticity level. The plasticity level at which performance was highest is referred to as the optimal plasticity level.

Optimal plasticity level was determined for different light regimes and different N availabilities in the soil. The light regimes all started at a light intensity of approximately $800 \mu\text{mol m}^{-2} \text{s}^{-1}$, which equals approximately 66% of the light intensity above the forest canopy on a clear day. In the first half of the growing season light availability decreased steeply, mimicking the light climate in a deciduous forest (see Equation 45 and Figure 7 in Chapter 2). The light intensity later in the season remained constant but differed between different light regimes to mimic different forest types. The N supply from the ambient soil is changed between simulations but was constant during the growing season.

To analyse the effect of differences in inherent growth rate between species all of the above simulations were repeated for four species that differed in Specific Leaf Area

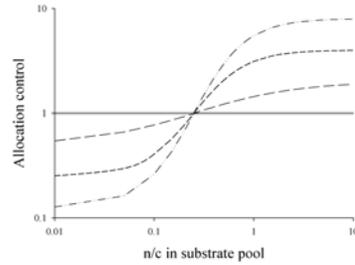


Figure 2 Shape of the allocation control function, reflecting the relation between n/c ratio in the substrate pool on the x-axis and the relative growth rate of aboveground biomass compared to the belowground biomass on the y-axis. Species with a higher plasticity level (indicated by the numbers on the right) can increase the aboveground growth rate stronger at the costs of the belowground growth rate at high values of the n/c ratio in the substrate pool; at low values of the n/c ratio in the substrate pool, the opposite is true.

(SLA), a plant trait that is closely related to the species potential growth rate (Poorter, 1991).

RESULTS

OPTIMAL PLASTICITY LEVEL

Growth of the model plant is determined by the availability of carbon and nitrogen in the substrate pool. As explained in chapter 2, at high concentrations of C and N growth is fast; if either one or both of the resources in the substrate pool is restricted, growth rate is slowed down. Growth rate is not determined by the availability of the most limiting resource but by a combination of the internal availabilities of both resources. Still, an increase in the concentration of the most limiting resource has the largest effect on the plant's growth rate. This is illustrated in Figure

1. The plastic plant has the capability to decrease the limitation of the most limiting resource by increasing the growth rate of the compartment involved in the uptake of that resource. However, the increase in the growth rate of one compartment occurs at the cost of the growth rate of the other compartment, so an increased allocation to either one results in a proportionally decreased allocation to the other compartment and thus to a decreased uptake of the resource acquired by this compartment (Figure 2). With this in mind the effect of plasticity on biomass production can be analysed.

From Figure 3, representing simulations in a light environment decreasing from $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ to $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ and low nitrogen supply in the soil ($n_a = 0.01$), it can be concluded that in terms of total plant mass after 150 days an optimum in plasticity level can be found. The Specific Leaf Area of the species was set to $0.005 \text{ m}^2 \text{ g}^{-1}$. At a plasticity level of nearly four, so a potential four-fold difference in growth rate of the two compartments, the plant possessed the highest biomass at the end of the growing season; both a lower and a higher level of plasticity resulted in a lower biomass production. In Figure 4 the carbon and nitrogen availability factors for growth of three species differing in plasticity level is given. The species represent A) the species with the optimum plasticity level (3.72) in the simulations of Figure 3, a species with B) a higher plasticity level (8.1), and C) a lower plasticity level (2.0). Because light availability is high in the beginning of the simulation and nitrogen supply from the environment is low, the nitrogen availability factor decreased strongly

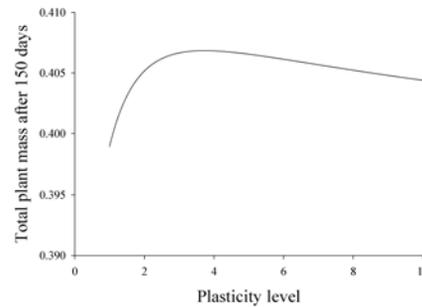


Figure 3 Total plant mass after 150 days of growth of species differing in plasticity level, as defined in the methods section. SLA of all species was set to 0.005. Growth was simulated in a light regime decreasing from $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ and at low nitrogen supply ($n_a = 0.01$).

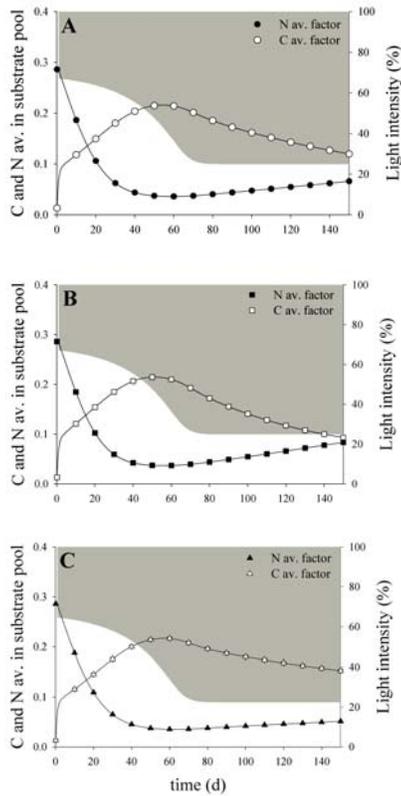


Figure 4 Carbon (open symbols) and nitrogen (filled symbols) availability factors over time of three species differing in plasticity. A) Optimal plasticity level (3.72), B) too high plasticity level (8.1), and C) too low plasticity level (2.0). Environmental settings as in Figure 3.

from the start of the growing season. After approximately 15 days the curve of the N availability factor crosses that of the C availability factor, and N was limiting growth more.

Consequently, all three plants start steering their shoot-to-plant ratio down (Figure 5) resulting in a slow down of the decrease in nitrogen availability. The species with the highest plasticity level most strongly reduced N limitation in the high light phase (Figure 4B). The minimum value of the N availability factor was 0.03642 and was reached after 55.5 days, while the species with the optimal plasticity level and the lowest plasticity level reached levels of 0.03582 and 0.03527, respectively, after 59.1 and 62.9 days. However, belowground investment occurred at the cost of aboveground growth and when light availability decreased later in the season growth of the species with the highest plasticity level was fastest (after 51.1 days, compared to 54.3 and 57.3 days for the other two species) and most strongly hampered by C availability (C availability factor of 0.2145, compared to 0.2158 and 0.2168). Of course this species, possessing the highest plasticity, could also correct its shoot-to-plant ratio fastest in the low light phase but due to the low light availability growth was slow and thus the alteration of the shoot-to-plant ratio was also slow. The species possessing the optimal plasticity level did reduce N limitation in the high light phase but

without inducing a strong carbon limitation in the low light period later in the season. Although differences in C and N availability factors and shoot-to-root ratio were small, they were sufficient to engender the differences in total plant mass shown in Figure 3.

EFFECT OF LIGHT REGIME

The optimal plasticity level for a species with $SLA = 0.005 \text{ m}^2 \text{ g}^{-1}$, grown at low nitrogen availability ($n_a = 0.01$) was determined for different light regimes, all starting at a light availability of approximately $800 \mu\text{mol m}^{-2} \text{ s}^{-1}$ of the light availability above the forest canopy but decreasing to a range of different light levels. The results are shown in Figure 6. The optimal plasticity level increased with an increase in the amount of light in the

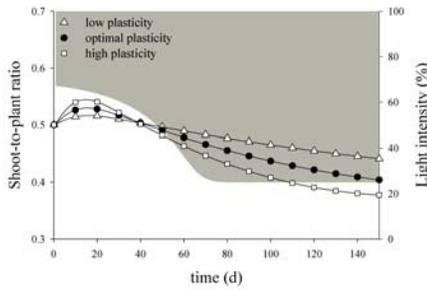


Figure 5 Shoot-to-plant ratio over time of a with the optimal plasticity level (3.72), a too high plasticity level (8.1), and a too low plasticity level (2.0). Environmental settings as in Figure 3.

latter part of the season and therefore with a reduction in the change in light intensity. Thus, optimal plasticity level was positively correlated to the light availability later in the season.

As explained above the optimal plasticity was determined by the balance between an adjustment to the high light period in the beginning of the growing season and to the low light period later in the season. A too slow change in shoot-to-plant ratio, caused by a too low plasticity, reduced the nitrogen limitation of growth in the high-light period too slowly, while a too fast change in shoot-to-plant ratio

entailed a strong carbon limitation in the low-light period later in the growing season. The lower the light intensity later in the season, the stronger the growth limitation and the more negative the effect of adjustment of the shoot-to-plant ratio in the first part of the growing season. At light levels below $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ later in the season, a plasticity level of one, so a rigid species, was found to produce the highest biomass.

As can be seen in Figure 7, showing the shoot-to-plant ratio (A) and the carbon and nitrogen availability factors of a rigid (B) and a plastic (C) species in a light regime that decreased to $120 \mu\text{mol m}^{-2} \text{s}^{-1}$, growth of the rigid species was slightly more N limited in the high light period but the C availability factor not only decreased slower than in the plastic species, the decrease also started later and did not reach the low value that was reached in the plastic species (Figure 7A and B). This caused the rigid strategy to be more profitable under these conditions.

To summarize, the light availability later in the season was positively related to the optimal plasticity level. So, the smaller the decrease in light intensity over the season, the higher the plasticity level at which optimal performance was found. A (too) strong decrease in shoot-to-plant ratio, as an adjustment to the initial high light intensity, caused severe C limitation in the low-light phase later in the season; the stronger the decline in light intensity and thus in photosynthetic rate, the larger the negative effect of high plasticity.

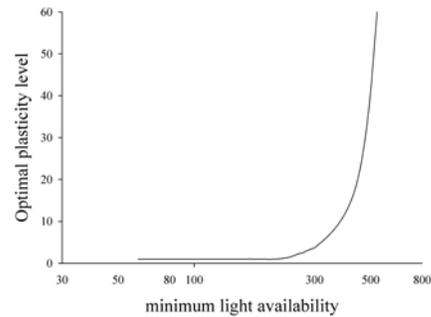


Figure 6 Optimal plasticity level, as defined in the method section, for a species with $\text{SLA} = 0.005$, grown at low nitrogen availability ($n_a=0.01$) and different light regimes. All light regimes started at $800 \mu\text{mol m}^{-2} \text{s}^{-1}$, the light intensity shown on the x-axis represents decreased light availability later in the season.

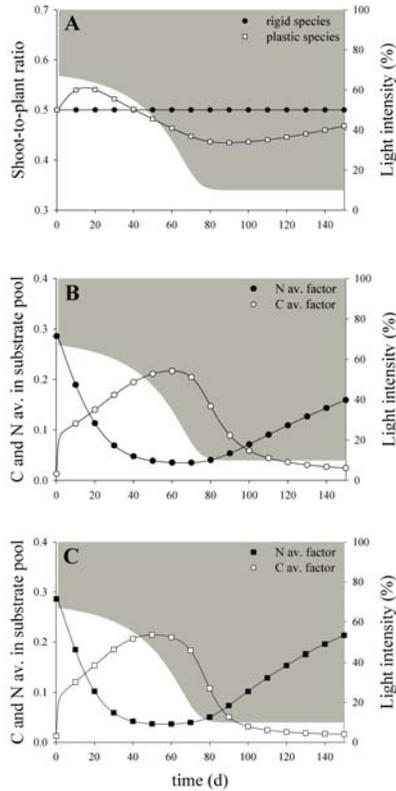


Figure 7 A) Shoot-to-plant ratio of a rigid species with plasticity level = 1.0 (circles) and a species with plasticity level = 8.1 (squares). B) Carbon (open symbols) and nitrogen (filled symbols) availability factors of the rigid species in time, and C) of the plastic species. Growing environment: low nitrogen availability ($n_a=0.01$) and a light regime decreasing from 800 to 120 $\mu\text{mol m}^{-2} \text{s}^{-1}$. SLA = 0.005.

EFFECT OF NITROGEN SUPPLY

The previous simulations showed that an initial decrease in shoot-to-plant ratio as plastic adjustment to high light and low N conditions in the environment in the beginning of the growing season caused a (too) strong carbon limitation of growth later in the season in light regimes where light intensity decreased considerably. In this situation, the model selected for a rigid plant species. When light intensity later in the growing season did not decrease strongly, main allocation direction of a plastic plant could remain the same all through the growing season and plasticity was advantageous. A higher level of N supply in the soil will cancel out the need for a decrease of shoot-to-plant ratio in the high-light period and, consequently, the plant can start steering its shoot-to-plant ratio up from the start of the simulation and continue steering up in the low-light period. Like in the situation where the main allocation direction was towards root throughout the whole season, plasticity should also be favorable if, due to higher N supply, allocation direction is continuously to the shoot.

This is confirmed in Figure 8, which shows the optimal plasticity level of species grown at different levels of N supply in a range of light regimes. In general, the optimal plasticity level was positively related to the N supply in the environment. Two exceptions were found. Firstly, at the lowest N supply ($n_a = 0.01$) and high light availability at the end of the growing season extreme values of optimal plasticity level

were found. This is due to slow growth rates, caused by the low N supply, and the strong steering that was necessary. If initial shoot-to-plant rate was lower, so the steering required was smaller, less extreme values were found (data not shown). Secondly, if light availability later in the season was below the range of 100 to 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ the optimal plasticity level at intermediate N supply ($n_a = 0.05$) is much higher than that at high N supply ($n_a = 0.3$). These conditions both call for a strong increase in shoot-to-plant ration to release the carbon limitation of growth both in the high- and in the low-light phase. However, as can be seen in Figure 9, the shoot-to-plant ratio at the highest N supply changed faster than that at the intermediate supply, even though plasticity level was lower.

Discussion

This is due to the higher growth rate at higher N supply enabling a faster adjustment of the shoot-to-plant ratio.

The increased growth rate also caused the optimal plasticity level to decrease with increasing light intensity later in the season. The combination of high N supply and high light throughout the growing season resulted in an even higher growth rate and reduced the optimal plasticity level.

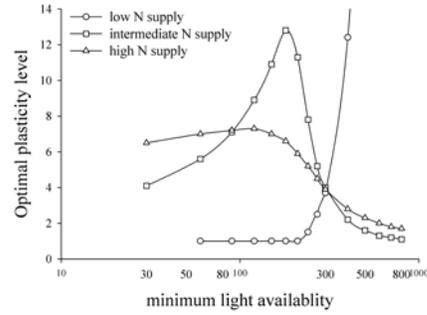


Figure 8 Optimal plasticity level, as defined in the methods section, of species adapted to different levels of N supply and in different light regimes. The circles represent the lowest N supply ($n_a=0.01$), the squares an intermediate level ($n_a=0.05$), and the triangles the highest level ($n_a=0.3$). Light availability shown on the x-axis represents the lower light availability later in the growing season.

EFFECT OF SPECIES INHERENT GROWTH RATE

The higher the growth rate of the plant, the faster it can adjust its shoot-to-plant ratio to the growth environment. A high growth rate can be brought about by favorable conditions, i.e. high resource supplies, but species can also differ in their inherent growth rate. Thus, the optimal plasticity level is expected to be different for species differing in inherent or potential growth rate. In Figure 10 the optimal plasticity level of three different species is shown for different levels of N supply over a range of light regimes. The species with the lowest Specific Leaf Area (SLA) had the lowest inherent growth rate, the species with the intermediate SLA, an intermediate growth rate and the species with the highest SLA the highest growth rate. As expected, the optimal plasticity level of the species with the lowest inherent growth rate was highest; the species with the highest potential growth rate needed to be the least plastic in the same situation.

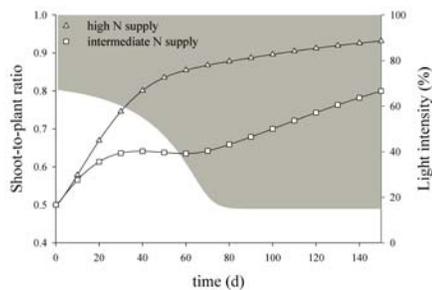


Figure 9 Shoot-to-plant ratio at the intermediate N supply ($n_a=0.05$; squares) and the high N supply ($n_a=0.3$; triangles) in a light regimes decreasing from 800 to 180 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Both species possess the plasticity level (defined in the method section) that is the optimum in the environment they are grown in.

DISCUSSION

A widely used definition of plasticity is ‘environmentally induced variation in the development of an organism’ (e.g. Bradshaw, 1965). However, the environment can affect the variation in the development of an organism in two different ways. Firstly, the environment can induce a functional response in a trait, enabling plants to improve or maximize their performance. Such a response

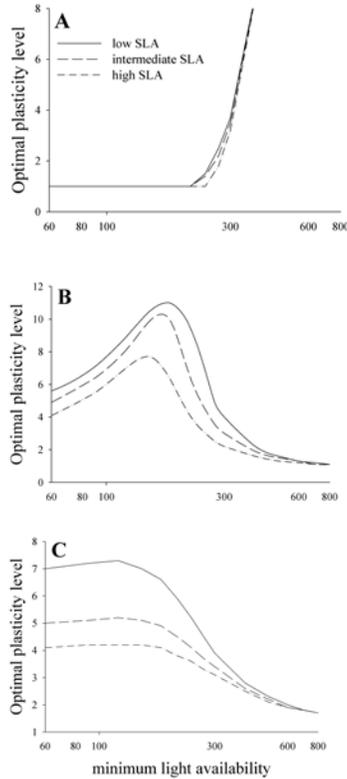


Figure 10 Optimal plasticity level, as defined in the methods section, of species differing in SLA. The solid line represents the species with the lowest SLA (0.005), the long-dashed line the species with an intermediate SLA (0.006), and the short-dashed line the species with the highest SLA (0.008). Optimal plasticity level was determined over a range of light regimes for A) low N supply ($n_a=0.01$), B) intermediate N supply ($n_a=0.05$), and C) high N supply ($n_a=0.3$).

is generally regarded as being adaptive (Sultan & Spencer, 2003). The optimal plasticity level used in the model simulations of this study as defined in the methods section can be regarded as a functional adaptation to adjust the ratio of resource acquisition to the need of the plant. Secondly, the environment can affect the rate of ontogenetic development of individuals (Coleman *et al.*, 1994; Huber & Stuefer, 1997). Differences observable after a certain period of time are simply a consequence of differences in developmental stage between plants from different environments. This was also observed in the model simulations, which showed that the same (functional) plasticity level had a different effect on the development of the shoot-to-plant ratio under different circumstances (e.g. Figure 8). A fast change in shoot-to-plant ratio under favorable conditions is not per definition a reflection of a high plasticity level but the result of complex interactions between aspects of growth (biomass production), morphogenesis (functional plasticity) and ontogenetic development. So, the model results indicate that both processes play a role in the plastic response in shoot-to-plant ratio to environmental changes, and this also is widely found in experimental studies (e.g. Aerts, 1994; Brouwer, 1962a; Corré, 1983). Furthermore, under favorable conditions aspects of growth and ontogenetic development played a more important role, enabled a fast change in shoot-to-plant ratio and a lower (functional) plasticity level was needed to obtain the maximum net biomass production at the end of the growing season.

This study aimed at investigating whether or not functional plasticity is advantageous under different environmental conditions. The results showed that functional plasticity is unfavorable if the main direction of allocation (to above or belowground biomass) in the first phase of the growing season is opposite to that later in the season; in other words if the resource that most limits growth differs drastically between two phases in the growing season. The growing conditions in the beginning of the season, as detected by the model plant, did not reliably indicate the conditions later in the growing season; the predictability of the environment was low (Levins, 1968; Schlichting & Pigliucci, 1998;

Via *et al.*, 1995). Unpredictable environmental variation has been hypothesized to select for a low plasticity (Alpert & Simms, 2002; Stuefer, 1997). Furthermore, a lower functional plasticity level was required when both light intensity and nitrogen supply were high during the full growing season. In this situation fast growth was possible and, as suggested above, aspects of growth and ontogenetic development brought about a fast adjustment of shoot-to-plant ratio reducing the role of functional plasticity. Functional plasticity showed to be advantageous when growth was most limited by the same resource all through the season.

A myriad of models simulating biomass allocation to shoots and roots is available in literature. Roughly three main approaches can be distinguished: empirical models, functional equilibrium models and sink regulation models (Marcelis, 1993; Thornley & Johnson, 1990). Empirical models can adequately simulate the system which it is calibrated for. However, application of the model to other conditions requires re-parameterization of the model. These types of models thus are not suitable for studying the role of plasticity under different conditions (Marcelis *et al.*, 1998). Functional equilibrium models are optimization models in which biomass distribution is related to the ratio of the C:N concentration in the plant. A disadvantage of these models is that biomass distribution is analyzed in the equilibrium situation and the processes affecting the development of shoot-to-plant ratio are not included in the analysis. Functional equilibrium models may fail to simulated ontogenetic effects or effect of dynamically changing growth conditions (Thornley, 1995). The third approach, modeling sink regulation, assumes biomass partitioning is regulated by sink strengths of the organs. The sink strength then can be defined as the potential growth rate of the organ, i.e. the growth rate under conditions of non-limiting assimilate supply. These models aim at a full understanding of allocation processes in the plant but their application is limited due to their complexity and difficulties to determine the parameters (Marcelis, 1993; Thornley, 1998). The model used in this study can be considered as a combination of the two last approaches. The potential growth rate of an organ changes in time and is dependent on the ratio of the C:N concentration in the plant, which represents processes of ontogeny and reflects the resource availability in the environment. Allocation processes are exclusively steered by the resource economy (both acquisition and use) of the plant. Therefore, this model is particularly suitable for investigating the relation between growth processes, resource availability and the need for plasticity.

In the understory of deciduous forests three distinct strategies are found to cope with the temporal period of (very) low light levels (Grime, 1979). The first strategy is shade - avoidance. Shade-avoiders complete their growth cycle before the tree layer has formed a closed canopy, viz. spring geophytes. These species are not included in this study. The second strategy is shade-tolerance. Species can tolerate shade and compensate for the low

light availability by plastic adjustments of their morphology (Grime, 1979). The model simulations showed that these species are characteristic for lightly shaded, relatively nutrient-rich environments, which may be found at better-lit spots in open forest woodlands and the forest edges. The third strategy is adaptation to shade to survive the deepest shade. The model showed that a rigid allocation strategy was the best strategy to survive very low levels of light availability later in the season, especially when nitrogen supply was low.

Chapter 5

Light, nutrients and the growth of herbaceous forest species: an experiment

ABSTRACT

The herb layer of forests planted on former agricultural land often differs from that of old-growth forest. This study investigates if the expected increased nutrient availability in the shaded conditions of newly planted forests and the plasticity of the species to adjust their biomass allocation to different levels of light and nutrients help explain these differences in the herb layers of the two forest types. In a greenhouse experiment biomass distribution and production of two species characteristic for the highly shaded forest floor, *Circaea lutetiana* and *Mercurialis perennis*, and two species more common in the forest edge, *Aegopodium podagraria* and *Impatiens parviflora* were studied at different levels of light (2, 8 and 66% of the full light level) and nutrients (30 kg N ha⁻¹ yr⁻¹ and 300 kg N ha⁻¹ yr⁻¹). The main factor affecting allocation and biomass production was light availability. Nutrient supply only had a significant effect at the higher light levels. Species were mainly plastic to changes in light and the two species from the forest floor showed to be more rigid in allocation pattern than the species from the forest edge. So, although the species from the forest edge were more plastic, they did not profit from the increased nutrient supply because the main factor affecting biomass distribution and production was light availability.

Keywords: Aegopodium podagraria, Afforestation, biomass allocation, Circaea lutetiana, forest herbs, Impatiens parviflora, light, nutrients, Mercurialis perennis, plasticity.

INTRODUCTION

In most countries of the European Union, large areas of agricultural land are taken out of production and converted to forest. The tree layers are generally planted at the time of agricultural abandonment, while the herb layer is commonly left to spontaneous development (Verheyen, 2002). Vegetation studies found distinct floristic differences between primary forests and forests on land that has been in agricultural use. In the newly planted forest the abundance of highly-competitive, nutrient-demanding species, normally occurring in the forest-edge, is higher and the occurrence of species characteristic for old-growth forest lags behind (e.g. Glitzenstein *et al.*, 1990; Koerner *et al.*, 1997; Honnay *et al.*, 1998). What causes these differences is subject to discussion. One of the factors that might play a role is habitat quality (Honnay *et al.*, 1999). Light, a main determinant of plant growth, is scarcely available on the forest floor habitat during the summer period. Besides light, nutrient availability also plays an important role in growth. In the forests planted on former agricultural land, nutrients are expected to be in ample supply. But, due to the low light conditions on the forest floor, the amount of carbon the plants have available for growth will be small, so the nutrient demand for growth will also be small. Therefore, the constraints of low light conditions on growth are expected to be sufficient to mask all effects of differences of nutrient availability. Meekings & McCarthy (2000) also pose this hypothesis based on the results of their study on the biennial forest herb *Alliaria petiolata*.

Peace & Grubb (1982) conclude from preceding research by other authors that a higher availability of mineral nutrients somehow allows plants to persist at lower levels of irradiance. The results of their study on *Impatiens parviflora* correspond with that conclusion. They found that addition of fertilizer increased dry weight yield at both high and low levels of irradiance in a controlled environment experiment. Peace (1984) documented this effect for 9 out of 10 species of forest herbs studied in southwest Germany (ref. in Coomes & Grubb, 2000). Since this phenomenon is not reported often in literature, Peace & Grubb suggested that it might be exclusive to strongly shade-tolerant species.

Although these results are counterintuitive the proposition of Peace & Grubb is an interesting idea. Knowledge of the response of forest species to variation in light and nutrient availability might help predicting the development of the herb layer of forests planted on former agricultural land.

The effect of light and nutrient supply only partly acts directly upon growth rate. Growth is also affected via resource allocation. Plants are capable of changing the biomass allocation and leaf morphology in such a way that resource capture is adjusted to the growing conditions, e.g. at low light conditions, plants can increase biomass allocation to the leaves and increase the Specific Leaf Area (SLA in $\text{cm}^2 \text{g}^{-1}$) while at low nutrient conditions an increased allocation to the roots is common (Aerts, 1994; Brouwer, 1962a; Evans & Poorter, 2001; Knops & Reinhart, 2000). This implies that in order to benefit from an increased nutrient availability species have to possess a high plasticity in biomass

allocation. However, in the forest understory variability of the environmental conditions is low and thus selection pressure for high plastic responses has been assumed to be low. Species adapted to the forest floor habitat would thus be expected to be less plastic. In contrast, in the more varying environment of the forest edge, the costs of a high plasticity (DeWitt *et al.*, 1998) will pay off because the environment is more variable, rather large differences in light availability exist in time and space. Species from the forest-edge, such as *Impatiens parviflora*, the species studied by Peace & Grubb (1982), are therefore expected to have a high plasticity in resource allocation and should be capable of profiting from an increase in nutrient availability.

This paper reports on a greenhouse study of growth and allocation of two species capable of growing in deep shade, *Circaea lutetiana* and *Mercurialis perennis*, and two species characteristic for less shaded conditions, *Aegopodium podagraria* and *Impatiens parviflora*. Species are classified based on the Dutch Ecological Flora (Weeda *et al.*, 1987, 1988). The aim is to test the hypotheses that nutrient availability affects yield at low irradiance and that highly shade-tolerant forests species possess lower plasticity in biomass allocation in response to light and nutrient availability as compared to more light-demanding species of the forest edge, and thus are less capable of taking advantage from increases in either irradiance or nutrient availability.

MATERIAL AND METHODS

Each of the four species was collected from a single natural population in the Netherlands in the spring of 2001. For each species, individuals of the same size-class were selected to standardize for plant size. Next, they were planted in plastic pots (20 cm in depth, 24

Table 1. Overview of used light-nutrient treatments

	Light		
	2%	8%	60%
High nutrient	2h	8h	60h
Low nutrient	2l	8l	60l

cm in diameter) filled with river sand. To provide nutrition during the period before the start of the experiment, plants were irrigated with a 0.4% solution of liquid fertilizer (EasyGro, 7-7-7). After 4 weeks, plants of each species were randomly assigned to one of six light-nutrient treatments presented in Table I and put in greenhouses in the botanical gardens of Utrecht University. The simulated canopy shade of 8% of the full light level was imposed by the use of one layer of a plastic green film (Lee Colortran International, Andover, UK; film no. 122, fern green) fixed to a layer of EVA tunnel foil, one layer of 50% shade cloth and one layer of 25% shade cloth (Maasmond, De Lier, The Netherlands). For the 2% light treatment, one layer of 70% shade cloth was added. Besides reducing the light availability, the green film also reduced the red:far red ratio from 1.1 in unshaded conditions to 0.21. The greenhouses of the control light treatment were covered with only a layer of the transparent EVA tunnel foil, which reduced the light

Table 2. Univariate ANOVA of the effect of light intensity (Li) and nutrient supply (Nu) on the total dry weight and allocation parameters of four forest species (Sp)

Effect	df	MS	F	
Total dry weight^a				
Light	2	19.349	166.982	**
Nutrients	1	0.616	5.319	*
Species	3	11.271	97.268	**
Li x Nu	2	0.492	4.246	*
Li x Sp	6	1.334	11.508	**
Nu x Sp	3	0.067	0.583	ns
Li x Nu x Sp	6	0.028	0.250	ns
Specific Leaf Area^a				
Light	2	5.918	519.912	**
Nutrients	1	0.056	4.963	*
Species	3	3.608	317.005	**
Li x Nu	2	0.058	5.166	**
Li x Sp	6	0.183	16.096	**
Nu x Sp	3	0.007	0.677	ns
Li x Nu x Sp	6	0.024	2.151	ns
Leaf Mass Fraction^b				
Light	2	0.409	52.863	**
Nutrients	1	0.211	27.307	**
Species	3	0.625	80.759	**
Li x Nu	2	0.023	3.074	*
Li x Sp	6	0.155	20.082	**
Nu x Sp	3	0.007	0.920	ns
Li x Nu x Sp	6	0.004	0.569	ns
Root Mass Fraction^b				
Light	2	0.789	48.426	**
Nutrients	1	0.391	24.000	**
Species	3	6.687	410.401	**
Li x Nu	2	0.072	4.446	*
Li x Sp	6	0.202	12.383	**
Nu x Sp	3	0.020	1.240	ns
Li x Nu x Sp	6	0.016	0.996	ns
Stem Mass Fraction^b				
Light	2	0.063	7.272	**
Nutrients	1	0.000	0.020	ns
Species	3	2.387	272.411	**
Li x Nu	2	0.005	0.618	ns
Li x Sp	6	0.037	4.186	**
Nu x Sp	3	0.005	0.569	ns
Li x Nu x Sp	6	0.007	0.759	ns
N-content of leaves^a				
Light	2	2.382	186.666	**
Nutrients	1	0.834	65.392	**
Species	3	3.248	254.512	**
Li x Nu	2	0.258	20.227	**
Li x Sp	6	0.099	7.803	**
Nu x Sp	3	0.098	7.675	**
Li x Nu x Sp	6	0.018	1.429	ns

^a is log transformed

^b is arcsin-transformed

* is significant at 0.05

** is significant at 0.01

level to approximately 60% of light available outside the greenhouses. The fertilizer levels were set using slow-release fertilizer (Osmocote Plus 10% 5-6m, Grace Sierra International, Heerlen, the Netherlands), which provided a continuous availability of nutrients during the experiment. The low nutrient treatment corresponded to 30 kg N ha⁻¹ yr⁻¹ and the high was equivalent to 300 kg N ha⁻¹ yr⁻¹. Every 3 weeks, five times in total, four plants of each treatment were harvested. Soil was washed from the roots, and the plants were separated into leaves, stems, roots and inflorescences. The leaf area of the fresh leaves was determined. After oven-drying for at least 48 hours at 70°C, dry weights of all plant parts were determined. From these data, total dry weight, Specific Leaf Area (SLA), Leaf Mass Fraction (LMF in g leaf mass g⁻¹ plant biomass), Stem Mass Fraction (SMF in g stem mass g⁻¹ plant mass) and Root Mass Fraction (RMF in g root mass g⁻¹ plant biomass) were derived and used for further analysis. Dried leaf material was grinded and after destruction N-content (Total Kjeldahl N in mg cm⁻²) was determined using a continuous-flow auto-analyzer (Skalar SA-40, The Netherlands). The first four harvests were used to qualitatively monitor the

Results

development of growth and allocation of the plants in the experiment, the fifth harvest was used to analyze the differences in yield between the treatments per species.

Plasticity is defined as the extent to which a plant can vary in a certain trait in response to light and nutrient availability. In order to calculate plasticity the average value of SLA, LMF, SMF, RMF and N-content was calculated in the fifth harvest for each of the six light-nutrient treatments. Per trait, plasticity was then expressed as the ratio between the highest and the lowest average value found in the six light-nutrient treatments.

A univariate ANOVA was computed for each dependent variable to test for main effects and interactions. To allow for normal data distribution, data transformations were applied to all data sets (see Table II).

RESULTS

As expected, an increase in both light and nutrient level had a significant positive effect on total yield in the fifth harvest (Figure 1). Table II displays the results of the univariate ANOVA on the total dataset. From this table it can be derived that the impact of light was larger than that of nutrients. Also an interactive effect of light and nutrients was found. This should be interpreted as a decreasing effect of nutrient supply on yield with decreasing irradiance. This can also be derived from Figure 1, the effect of increased nutrient supply was much stronger under high light conditions than at the lower light levels. Nutrient supply had a significant effect on yield in the 60% light treatment, but no effect in the 8% and 2% light treatments (data not shown).

The species factor explained a large part of the variation in yield in the fifth harvest (Table II). This was caused by differences in absolute values of final yield between the species. At high light availability *Circaea* and *Aegopodium* had the highest biomass, at low light levels, *Circaea* and *Impatiens*. *Mercurialis* had low biomass production across the light treatments (Figure 1). The reaction pattern to light, nutrients and light x nutrients as described above, did not differ principally between the species (Figure 1).

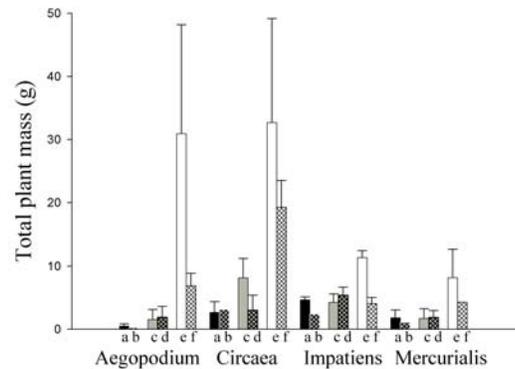


Figure 1. Mean total biomass at the fifth harvest for each species at a) high nutrient treatment and b) low nutrient treatment at 2% light, c) high nutrient treatment and d) low nutrient treatment at 8% light, and e) high nutrient treatment and f) low nutrient treatment at 60% light. The error bars represent the standard deviation.

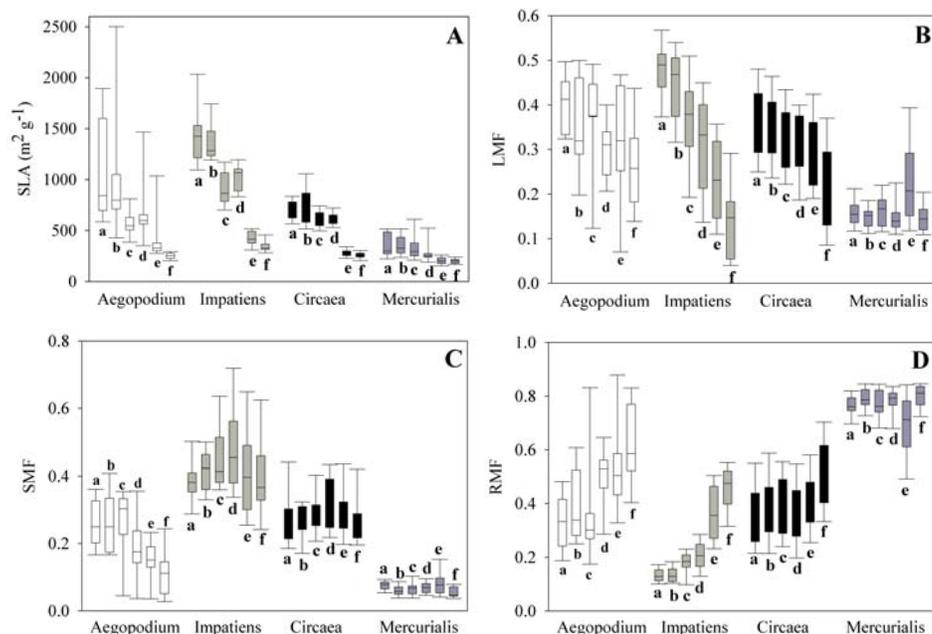


Figure 2. Average values of (A) Specific Leaf Area, (B) Leaf Mass Fraction, (C) Shoot Mass Fraction, (D) Root Mass Fraction per species at a) high nutrient treatment and b) low nutrient treatment at 2% light, c) high nutrient treatment and d) low nutrient treatment at 8% light, and e) high nutrient treatment and f) low nutrient treatment at 60% light. The error bars represent the standard deviation

The results of SLA, LMF, RMF and N-content showed a similar, though less pronounced, pattern in reaction to light, nutrients and light x nutrients as did yield (Figure 2 and 3). Again, light was the most important determinant. An exception to this pattern was found in SMF that showed an effect of light but no clear effect of nutrients. In general, SLA, LMF and leaf N-concentration increased with decreasing light and increasing nutrient supply. For RMF in all species, except *Mercurialis*, the opposite relation was found, an increase with increasing light and decreasing nutrient level. Total Leaf Area showed a positive correlation with both irradiance and nutrient supply. As for yield, the species factor also explained a large part of the variation in the data sets of SLA, LMF, SMF, RMF and N-content (Table II); there were large absolute differences between species in their biomass distribution and SLA. In general, the highest values of SLA and SMF were found for *Impatiens*, the lowest for *Mercurialis* independent of treatments (Figure 2A,C). For RMF these rankings were reversed (Figure 2D). For LMF species ranking did differ between treatments. At low light levels the highest values were found for *Impatiens*, the lowest for *Mercurialis*. At high irradiance LMF of both *Impatiens* and *Mercurialis* were ranking lowest (Figure 2B).

Species and light availability were the most important variables affecting the N-content of the leaves (Table II). Plants grown at high light availability had higher nutrient concentration per leaf area than plants grown at low light availability (Figure 3). A similar effect was found for nutrient supply.

As shown in Table II a significant effect of light x species, but not of nutrient x species, was found for all plant traits. This can be interpreted as differences in plasticity to irradiance between the species. Between the 2% and 8% light treatments, all species showed low plasticity and no differences in plasticity were found between species (data not shown).

Table III presents the plasticity in allocation calculated over all treatments. The species were most plastic in SLA. *Impatiens* and *Aegopodium* showed the highest plasticity in all allocation traits, but this did not translate into high differences in yield in the different treatments. *Mercurialis* showed the lowest plasticity in all traits. *Circaea* also showed low plasticity in allocation traits but for this species high differences in yield were found between the treatments.

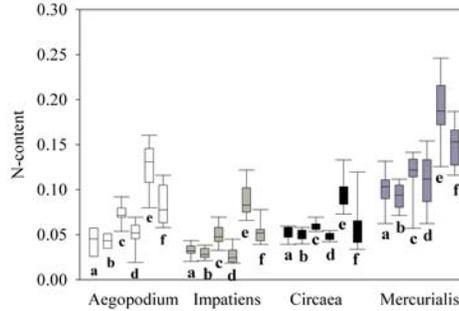


Figure 3. Leaf N-content (in mg.cm-2) per species at a) high nutrient treatment and b) low nutrient treatment at 2% light, c) high nutrient treatment and d) low nutrient treatment at 8% light, and e) high nutrient treatment and f) low nutrient treatment at 60% light. The error bars represent the standard deviation.

DISCUSSION

In this study two hypotheses were tested. The first hypothesis, that nutrient availability affects yield at low irradiance, was not supported by the data presented in this paper. The prime factor affecting growth was irradiance and the effect of nutrient availability was only evident when sufficient light for substantial growth was available (Figure 1).

Consequently, no evidence was found for the suggestion of Peace & Grubb (1982) that a higher availability of mineral nutrients enables strongly shade-tolerant species to increase dry weight yield at low levels of irradiance. A possible cause for this difference may be found in the difference in growing conditions. While Peace & Grubb (1982) carried out

Table III Ratio between the highest and lowest average value of yield and allocation traits as a measure of plasticity per species

	SLA	LMF	SMF	RMF	N-content
Aegopodium	4.1	1.5	2.4	1.8	2.1
Impatiens	4.2	3.4	1.2	3.4	2.5
Circaea	2.8	1.7	1.2	1.4	2.4
Mercurialis	1.8	1.5	1.5	1.2	1.3

the experiment in controlled environment cabinets, the plants in this study were grown in greenhouses. In those greenhouses, light conditions were proportional

to the light conditions outside the greenhouse and would therefore fluctuate more during the experiment than under the controlled light conditions Peace & Grubb (1982) used. On a cloudy day, light conditions in the greenhouse could reach very low values, which would affect the growth of the plant. The suggestion of Peace & Grubb (1982) that highly shade-tolerant species are capable of increasing their dry weight yield at low light levels can thus be valid for moderately low light levels in controlled environment cabinets but not for the repeatedly very low light levels experienced in greenhouses on cloudy days, or analogous, on cloudy days under the forest canopy.

The data presented in this paper do support the second hypothesis. The two highly shade-tolerant species, *Circaea lutetiana* and *Mercurialis perennis*, showed a lower plasticity in allocation traits than the two forest-edge species, *Aegopodium podagraria* and *Impatiens parviflora* (Table III). A high plasticity is expected to enable plants to adjust to different growth conditions and minimize the negative effects of decreases in resources. In this study species were mainly plastic to changes in light so that in the more plastic species the proportional differences between biomass production in high light as compared to low light was less than in less plastic species. The decrease in yield of *Circaea* and *Mercurialis*, relatively rigid species, complied with the expected pattern. Figure 1 shows that biomass production at low light conditions of *Impatiens parviflora*, a highly plastic species, is approximately half the biomass production at high irradiance. However, low light biomass production of *Aegopodium*, also a highly plastic plant, was less than 1% of the production at the 60% light treatments. The general result that the species in this experiment were more responsive to light than to nutrient availability might be due to the fact that the light manipulations in the experiment spanned a larger range than the manipulations in nutrient availability. Overall, *Impatiens* seems to be the most variable of the four species. It also was the only annual used in the experiment. It is imaginable that for annual species, that don't have the opportunity to draw from the resource stock in their storage organ in adverse growing conditions, plasticity might be an essential trait to survive in variable environments.

Chapter 6

Summary and General discussion

PLANT TRAITS IN FOREST UNDERSTORY HERBS

A central idea in plant ecology is that plants are adapted to the potential offered by their habitat. Especially strategies to endure stressful environments, like the low-light conditions in the forest understory, have attracted much attention. Still, a clear and comprehensive definition of traits that characterize shade tolerant species from the forest understory cannot be given. Knowledge of these characteristics and the role they play in plant functioning and growth not only lead to a better understanding of the world around us but also enable predictions about the consequences of changes in growing conditions. The aim of this study is to describe the trait characteristics that facilitate optimal growth in the low-light conditions in the forest understory, compared to the characteristics favorable under relatively high light conditions. The study focuses on the role of two major plant traits that play an important role in plant growth processes: shoot-to-plant ratio and a suite of leaf functional traits, consisting of Specific Leaf Area (SLA), leaf longevity, and mass-based nitrogen concentration, photosynthetic capacity, and maintenance respiration rate. For the greater part, a modeling approach is followed. Modeling enables isolation of the role of the traits of interest on the growth of the plant and assessment of the adaptiveness of the trait. As a consequence, the relation between the patterns found and the trait that was varied is stronger and can be better explained.

A detailed description of the model is given in Chapter 2. The model plant consists of an aboveground and a belowground part and grows on carbon and nitrogen, acquired by the leaves and fine roots, respectively. It includes the logistic growth phase with accompanying realistic photosynthesis and N uptake processes. The model offers the possibility to define different species in terms of biomass allocation, leaf functional traits and levels of plasticity of these traits. The results showed a realistic biomass production, with a growth rate decreasing with size of the plant. Furthermore, the simulations demonstrated the role of the transition from exponential growth to logistic growth in the acquisition and demand of carbon and nitrogen and the consequences for the allocation processes in plants. This information provided a good basis for a thorough understanding of the growth processes in the model plant.

In Chapter 3 the model is used to evaluate the role of shoot-to-plant ratio and SLA, as representative of the suite of functional traits, in shade-tolerance. If light conditions were low, according to the model simulations the plant performed best with a low SLA and a high shoot-to-plant ratio. A low SLA is correlated to low biomass loss and low maintenance respiration, and was typified in this study as a conservation strategy. The role of minimization of biomass loss and maintenance respiration rate in net biomass production decreased with increasing light availability. The high shoot-to-plant ratio enabled a higher carbon gain and reduced the respiration costs of the belowground compartment. At higher light availability, carbon gain was higher, growth was faster and more nitrogen was needed to support growth, which caused the optimal shoot-to-plant ratio to decrease. Similar patterns were found at constant light and at a variable light regime mimicking the light availability in the understory of a deciduous forest.

Most plants are, to some extent, capable of a plastic response to changing growth conditions, however. Plasticity has been hypothesized to be more advantageous in habitats where resource availability is overall higher and that shows temporal variation at a scale that can be responded to by a plant within the (remainder of) the growing season. In Chapter 4 the question was addressed whether or not plasticity in shoot-root allocation is advantageous for plants adapted to the understory of deciduous forests. In deciduous forests in which the light availability is reduced to very low levels the model predicted, a low plasticity level or even a rigid allocation strategy to produce the highest biomass after 150 days of growth, especially when combined with low nitrogen availability; the contrast between the high light period at the beginning of the growing season and the low light period later in the season was too large to make plastic adaptation beneficial. Due to acclimation to the initial high light period the plants did not have sufficient aboveground biomass to fulfill the carbon demands of growth and maintenance in the severely shaded conditions later in the season.

Thus, according to the model simulations, a species from a dense (deciduous) forest should possess a low SLA, a high shoot-to-plant ratio and a low plastic response in shoot-root allocation to changes in light availability.

Under better lit conditions, for instance in the forest edge, the model predicted a higher SLA and a higher plasticity in biomass allocation to be a suitable adaptation. These

predictions are consistent with the experimental results presented in Chapter 5 where the SLA and shoot-to-plant ratio of four species, two from the forest interior and two from the forest edge, grown in different light and nutrient conditions, were compared. However, since only four species were used a more extensive study of those traits in shade-tolerant understory species and species from better-lit places would be valuable to test the model results.

ASSUMPTIONS AND APPROACHES

Ecologists assume that natural selection tends to maximize the fitness, or the genetic contribution to future generations, of an individual. In this study plant performance is measured as net biomass production in one growing season of 150 days and the optimal strategy, assumed to be favoured by selection, is the strategy at which performance is highest. Reproductive strategy was not included in the functional analysis of the model simulations. Because both the quantity and the quality of reproductive output are highly correlated to biomass production, fitness of a plant can be viewed as a function of its biomass production (Bloom *et al.*, 1985). For the purpose of this model study biomass production was a suitable measure.

In this study the model was used to test hypotheses about the role of several plant traits in shade tolerance and plant performance under different environmental conditions. The model proved to be a suitable tool for this purpose. Firstly, it provided straight forward results and clear patterns for the adaptation of plants to a range of light regimes. Secondly, the model results provided an explanation of how (plasticity in) shoot-to-plant ratio and leaf functional traits affect growth and the consequences of that under different light and nitrogen conditions. Thus, both hypotheses about mechanisms and plant growth processes as well as hypotheses about the patterns resulting from that were tested. This provides a valuable contribution to the understanding of growth processes at low light conditions and enables definition of different strategies in different environments.

Model results were mainly analysed in terms of patterns. To estimate exact values of species traits in different conditions, the model is less suitable.

Besides in hypothesis-testing, models can also be used to assess the effect of environmental change or management programs. The agreement between modelling results and the data collected in the experiment creates possibilities for the use of the model in predictive studies. In the model, different species can be defined that can be viewed as representatives of ecological groups (e.g. shade-tolerant forest species) and their response to, for instance, increased nitrogen availability can be tested.

A model is, by definition, a simplification of a system (Jørgensen & Bendricchio, 2001). This simplicity represents the major strength of the use of models in the study of complex systems. However, it is important to be conscious of the limitations of the model. In the

model developed in this study, the loss of biomass is not implemented as shedding of complete units but as a fixed fraction of the existing biomass that is lost every time step. This not only kept the model structure relatively simple but also prevented jerky changes in the plant's status. The consequence of the use of a fixed biomass loss fraction is an overestimation of the biomass loss for young biomass but an underestimation for older biomass. When leaves in the lower parts of the shoot become heavily shaded by the leaves above, plants tend to increase the shedding of the lower leaves. This functionality is lacking from the model. However, this is only an issue at the higher light levels where biomass production is fast. The consequences have been discussed in Chapter 3. Both the shoot and the root can only grow in height. The diameter of the cylinders is fixed. Would the model plant have the possibility to change its diameter, enabling it to spread out its leaves, it would have a tool to prevent self-shading when a large canopy has formed. Especially at lower light conditions horizontal expansion may be an advantageous strategy and extension of the model to evaluate the consequences of diameter growth will be an interesting extension.

To conclude with, in the model light only falls on top of the plants. Diffuse light and diagonal light beams are not included. It is debatable to what extent this assumption deviates from the light availability in reality. However, this assumption enabled an important simplification of the model system.

A more complex model would not have led to a better insight. With increasing complexity of the model the results would also have become more complex and the interpretation would have been less straight forward. However, when interpreting the simulation results of the simplified model or considering questions to be asked, it is wise to keep in mind the limitations of this model.

OTHER TRAITS SUPPORTING SHADE-TOLERANCE

In the understory a large variety of species is found that all possess a unique set of traits that not only define them as different species but that enable them to survive and thrive in their habitat. Apart from spring geophytes and winter-annuals, all these species have adapted to (a period of) low light conditions at the forest floor. In this study, the role of two plant traits, shoot-to-plant ratio and the suite of leaf functional traits, in this adaptation have been evaluated. However, besides those two traits, species from the forest understory do have more traits in common.

For instance a considerable number of forest herbs exhibits an evergreen leaf habit (Bierzychudek, 1982). This trait can be compared to increased leaf longevity, which was shown in Chapter 3 to be favorable under low light conditions. Besides a prolonged period of photosynthetic C gain, an evergreen leaf habit entails some more advantages. Plants with evergreen leaves do not have to build up their photosynthetic system in spring every year and can start photosynthesizing immediately when conditions become suitable. Due to physical and biomechanical constraints evergreen leaves need to have a low SLA

to support their longevity and not to be damaged by the harsh winter-conditions. It can be expected that the same trade-off between conservation and acquisition will also play a role when an evergreen leaf habit is included in the strategies that can be followed. When (light) conditions are poor, the advantages of the evergreen strategy will be relatively high, while at better conditions, growth can be faster and investment in high carbon acquisition traits, related to a high SLA, excluding the option of keeping the leaves through the winter period, will lead to the highest biomass production.

Another trait that enables a fast start at the beginning of the growing season is a perennial life-history. Perennials have a large capacity for storage of both nutrients and carbohydrates, which enables these plants to start growth early and to survive unfavorable conditions (Lambers *et al.*, 1998). Storage of resources also enables the plant to survive (successive) periods of low light availability in the development of the forest ecosystem (Willems *et al.*, 1999). Obviously, the allocation of resources to storage has a future advantage but reduces the actual growth. Therefore, the advantage of perennality can only be evaluated in a long-term (population) context.

These traits, both aimed at conservation of biomass and acquired resources, can also be viewed as adaptations to low light conditions. Besides conservation of acquired resources forest plants also have ways to increase their resource gain. Many forest herbs exhibit clonal growth (e.g. Bierzychudek, 1982), enabling them to distribute their biomass at different locations in different levels of resource availability. The spatial spread of clonal plants, their capability for local resource uptake by the spatially separated ramets and their capacity for internal resource transport over considerable distances could give these species selective advantages in spatially heterogeneous environments (Stuefer, 1997) which the forest floor often is (Chazdon *et al.*, 1988; Lechowicz & Bell, 1991; Pearcy, 1983).

Furthermore, carbon gain can be increased by photosynthetic adaptation. Species from the forest understory have photosynthetic adaptations that enable efficient harvest of light in sunflecks. Sunflecks typically account for 40 to 60% of the total irradiance in understories of dense forests (Chazdon & Pearcy, 1991). Although most understory plants can maintain a positive carbon balance with diffuse light, sunflecks can increase the total carbon gain by 9 to 46% depending on their size and frequency (Lambers *et al.*, 1998). Efficient harvest of sunflecks thus can improve the plants carbon budget and will release the need to be conservative with acquired carbon resources. Thus, plants capable of clonal growth and/or harvesting sunflecks will be able to grow in deeper shade, allocate more to storage organs and may not need to possess extreme SLA-leaves.

This list is not complete; more plant traits play a role in shade-tolerance. However, this does not affect the value of the results presented in this study. The quantitative analysis of the role of shoot-to-plant ratio and leaf functional traits in growth processes under different conditions contributed to a better understanding of their relation with their growing environment and exceptions in the patterns described in this study will raise questions of how the plant compensates for the deviation. Furthermore, based on the

results and mechanisms presented in this study, the consequences of the above mentioned plant traits can be better estimated.

DEVELOPMENT OF THE UNDERSTORY OF FORESTS PLANTED ON FORMER ARABLE LAND

Now that a shade-tolerant species and a species from better-lit habitats can be defined in terms of (plasticity in) shoot-to-plant ratio and leaf functional traits, the effect of increased nitrogen deposition on a vegetation consisting of both types of species can be analyzed. For this a competition version of the model was used, simulating two plants growing in the same space, light and nitrogen. The parameters of the plant traits defining the two species, a forest and a non-forest species, are given in Table I. All other parameter settings were similar to those used in Chapter 3 and 4. The light availability falling on top of the two plants is reduced by the leaf area of both plants, resulting in a stronger decrease of the light intensity and thus lower light levels in the lower layers of the canopy. Consequently, the photosynthetic resource gain of both plants is reduced compared to that of a plant growing solitary. In the model, light availability and photosynthesis are integrated over the height of the canopy. The plant species has a higher stature and can place its leaves above the other plant can capture more light and, at the same time, reduces the light availability of the other plant. However, the two species differ in their capability to cope with low light conditions. The division of nitrogen is modeled in a similar way. The total amount of root mass reduces the N concentration in the depletion zone and thus reduces the rate at which nitrogen can be taken up by the plants. The plant that has the largest portion of root biomass can take up more nitrogen compared to the other species.

Table I Parameter values defining the two different species.

	Forest species	Non-forest species
SLA	0.0025	0.007
Shoot-to-plant ratio	0.7	0.5
Plasticity level	1.0	8.0

At constant low light conditions and low nitrogen availability, representing the natural situation in an evergreen forest, the forest species

produced the most biomass in a competitive situation. At a light availability of $30 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ the non-forest species could not survive and from a light availability of approximately $120 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and higher, the non-forest species produced the highest biomass (Figure 1A). Figure 1B shows the biomass production of the two species in competition when nitrogen level was increased. At low light conditions, below $120 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, plant growth of both species hardly profited from the increased nitrogen. The forest species remained the best performer. At higher light levels, however, the non-forest species was able to profit more from the increased N availability than the forest species.

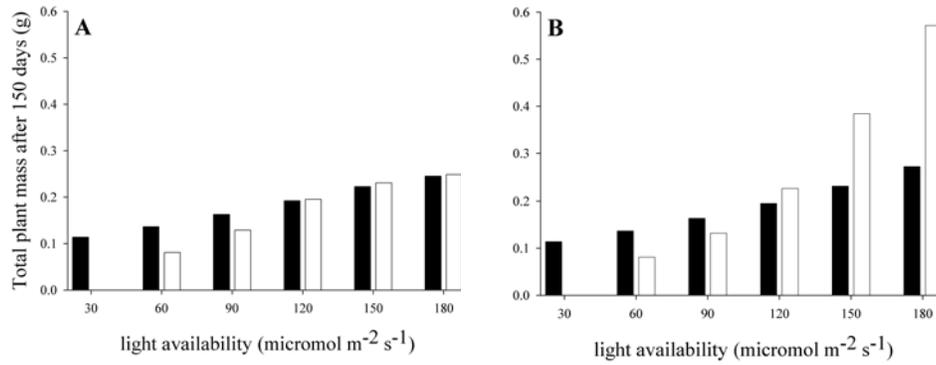


Figure 1 Total plant mass after 150 days of growth of a forest species (filled bars) and a non-forest species (open bars) growing in competition in the understory of an evergreen forest with A) low N supply ($n_a=0.01$) and B) increased N supply ($n_a=0.1$). On the x-axis, the light availability on the forest floor is given.

From these simulations it can be concluded that in the darkest forests, with light availabilities equaling up to 10% of the light availability above the forest canopy, non-forest species are not likely to invade the forest understory under influence of increased N availability.

The results agree with the hypothesis that has been brought forward before in this study that the constraints of low light conditions on growth are expected to be sufficient to mask all effects of differences in nutrient availability (Lameire *et al.*, 2000; Meekings & McCarthy, 2000). The same result was found in the experiment presented in Chapter 5. The prime factor affecting growth was light availability and the effect of nutrient availability was only evident when sufficient light for substantial growth was available.

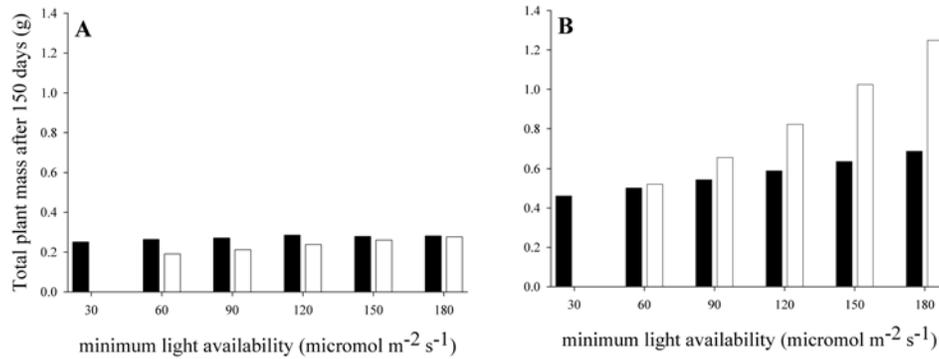


Figure 2 Total plant mass after 150 days of growth of a forest species (filled bars) and a non-forest species (open bars) growing in competition in the understory of a deciduous forest with A) low N supply ($n_a=0.01$) and B) increased N supply ($n_a=0.1$). On the x-axis, the light availability in the low light phase later in the growing season is given.

When light availability is high at the beginning of the growing season and decreases later on the results changed. The model simulations showed that at low nitrogen availability (Figure 2A) the non-forest species was not able to produce more biomass than the forest species in the deciduous forest regimes (decreasing to 30-180 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Although both species could profit from the higher N availability (Figure 2B), the non-forest species profited more, especially in the high-light phase in the beginning of the growing season and produced more biomass than the forest species. Only at the light regime decreasing to 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ the non-forest species could not survive the low light period and died. This implies that under a deciduous light regime highly competitive non-forest species are able to penetrate the forest interior under increased levels of nitrogen, except for forests in which the light level is severely reduced later in the growing season.

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Nederlandse Samenvatting

INTRODUCTIE EN METHODE

ACHTERGROND

Door een overschot aan graan en andere agrarische producten worden aanzienlijke hoeveelheden landbouwgrond uit productie genomen. De EU heeft besloten om op deze voormalige landbouwgronden de aanplant van bossen te stimuleren. Door de vastlegging van kooldioxide dragen bossen bij aan het verwijderen van broeikasgassen uit de atmosfeer. Het EU-project AFFOREST heeft onderzocht welke milieufactoren (vastlegging van kooldioxide, depositie en uitspoeling van stikstof en effect op grondwaterstand) door de aanplant van bos worden beïnvloed. Naast deze effecten op het milieu was ook de ontwikkelingsmogelijkheden van de ondergroei in deze nieuwe bossen onderdeel van het AFFOREST-project. De studie van dit laatste onderwerp heeft geleid tot het voor u liggende proefschrift.

De lage beschikbaarheid van licht wordt vaak genoemd als een belangrijke groeibeperkende factor voor de vegetatie in de bosondergroei. Op de bosbodem is de lichtintensiteit in elk geval een deel van het jaar laag. Daarnaast is de groei van planten in veel bossystemen ook gelimiteerd door de beschikbaarheid van stikstof.

Voorgaand onderzoek heeft aangetoond dat als gevolg van de toepassing van meststoffen tijdens agrarisch gebruik de beschikbaarheid van stikstof in bossen op voormalige landbouwgrond hoger is dan in natuurlijke bossen. Een verhoogde beschikbaarheid van stikstof kan leiden tot een verschuiving in de soortensamenstelling van de vegetatie, zoals bijvoorbeeld is beschreven voor veengebieden en klakgraslanden. Gegevens over de ontwikkeling van de ondergroei in bossen op verlaten akkers en weiland zijn schaars maar algemeen wordt aangenomen dat het voormalige landgebruik van invloed is op de ontwikkelingsmogelijkheden van de ondergroei in de nieuwe bossen. Deze verwachting wordt ondersteund door de verandering in vegetatiesamenstelling in natuurlijke bossen die onder invloed staan van verhoogde depositie van stikstof en andere voedingsstoffen. In deze bossen wordt een toename gevonden van snelgroeïende, competitieve soorten, die vaak worden aangemerkt als stikstofindicatoren.

De processen die ten grondslag liggen aan deze veranderingen en de rol die de beschikbaarheid van licht en stikstof hierin spelen zijn nog niet precies bekend. Om

voorspellingen te kunnen doen over de ontwikkeling van de ondergroei in nieuw aangeplante bossen op voormalige landbouwgrond en advies te geven voor inrichting en beheer is een goed inzicht in de interactie tussen planteneigenschappen, standplaats en groeiprocessen noodzakelijk.

PLANTENECOLOGISCHE BENADERING

Een algemene aanname in de plantecologie is dat natuurlijk selectie heeft geleid tot soorten met verschillende (sets van) eigenschappen die deze soorten in staat stelt te groeien in verschillende habitats.

De twee standplaatsfactoren waarop in dit onderzoek wordt gefocussed, licht (koolstof, C) en stikstof (N), worden opgenomen door verschillende compartimenten van de plant; licht door de spruit, stikstof door de wortels. De verdeling van biomassa tussen deze twee compartimenten, samen met de efficiëntie waarmee de stoffen kunnen worden opgenomen, bepaalt dan ook in welke verhouding C en N kunnen worden verworven.

Deze zogenaamde spruit-wortel verhouding houdt plantencologen al lange tijd bezig. De meeste planten kunnen hun spruit-wortel verhouding plastisch aanpassen aan hun standplaatsomstandigheden. Als het licht de groei beperkt vergroot de plant zijn spruit ten koste van de wortel, als stikstof minder goed beschikbaar is, investeert de plant meer in de wortels. Hoewel het patroon bij al deze planten hetzelfde is, worden grote verschillen gevonden in de mate van plasticiteit tussen planten. Natuurlijke selectie heeft niet onder alle omstandigheden geleid tot een grote plasticiteit. Hieruit zou geconcludeerd kunnen worden dat plasticiteit niet onder alle omstandigheden gunstig voor plantengroei. In het algemeen wordt aangenomen dat soorten van de bosondergroei minder plastisch zijn in hun spruit-wortel verhouding, dus dat plasticiteit in het bosmilieu niet een voordeel oplevert.

Een andere planteneigenschap die een belangrijke rol speelt in de groei van planten en die bij veel soorten een plastische reactie op licht (en stikstof) laat zien is het specifieke bladoppervlak (eng. Specific Leaf Area, SLA). Bladeren met een lage SLA zijn in het algemeen dikker en steviger, soorten met een hogere SLA hebben meer oppervlak per gram biomassa om licht op te vangen maar zijn ook dunner en kwetsbaarder. Onderzoek heeft aangetoond dat deze SLA is gekoppeld aan een aantal andere bladeigenschappen. Soorten met een lage SLA bezitten door fysische, morfologische en fysiologische beperkingen een lage stikstofconcentratie en als gevolg daarvan een lage fotosynthesecapaciteit (C opname) maar ook een lage onderhoudsademhaling (C kosten) en een lange levensduur. Een soort met een hoge SLA heeft een kortere levensduur en een hogere onderhoudsademhaling maar kan sneller koolstof opnemen door een hogere stikstofconcentratie en daarmee samenhangend een hogere fotosynthesecapaciteit. Binnen een soort wordt vaak een hogere SLA, dus een groter en dunner blad, gevonden bij individuen die in de schaduw zijn opgegroeid dan bij individuen die onder lichtere omstandigheden hebben gestaan. Recentelijk werd gesuggereerd dat verschillen tussen

soorten precies het omgekeerde patroon laten zien, dus een lagere SLA voor schaduwsoorten in vergelijking met soorten die zijn aangepast aan lichtere omstandigheden.

Hoewel veel ideeën bestaan over de eigenschappen die planten zouden moeten bezitten om te kunnen overleven onder schaduwrijke omstandigheden kan er tot dusver nog geen duidelijke en volledige definitie worden gegeven van de karakteristieken van schaduwtolerante soorten uit de bosondergroei. In deze studie is gekeken naar de rol van (plasticiteit in) spruit-wortel verhouding en specifiek bladoppervlak in de groei van planten onder verschillende omstandigheden en de verschillen die tussen verschillende soortengroepen bestaan.

METHODE

In de systematische analyse van planteneigenschappen in groeiprocessen kunnen mechanistische groeimodellen een waardevol rol spelen. Een model maakt het mogelijk de interactie tussen standplaats en een bepaalde planteneigenschap of een set van planteneigenschappen te bestuderen terwijl andere eigenschappen niet worden gevarieerd. Hiermee kunnen planteneologische hypothesen worden getest en waargenomen patronen worden verklaard. Het model dat wordt gebruikt in deze studie bouwt voort op het werk van Schieving (1998) en simuleert de opnamen en verdeling van koolstof (C) en stikstof (N) door een plant. Het bevat een eenvoudig maar realistisch lichtklimaat waarin de beschikbaarheid van licht op een bepaald punt in de spruit afneemt naarmate er meer bladlagen boven dat punt liggen. Op een vergelijkbare manier neemt de beschikbaarheid van stikstof in de bodem af met de groei van de wortelbiomassa. De verdeling van nieuwe biomassa over spruit en wortel wordt bepaald door de interne beschikbaarheid van C en N in de plant. Als de interne beschikbaarheid van C hoog is ten opzichte van de interne beschikbaarheid van N dan wordt een groter deel van de nieuwe biomassa in wortels geïnvesteerd om de N voorraad in de plant te vergroten; als de interne beschikbaarheid van C laag is gebeurt het omgekeerde. Een uitgebreide beschrijving van het model is gegeven in hoofdstuk 2.

Door de bladeigenschappen, de spruit-wortel verhouding of de plasticiteit in spruit-wortel verhouding te veranderen kunnen verschillende soorten worden gedefinieerd. Het model kan worden gebruikt om de eigenschappen waarmee maximale biomassa-productie wordt bereikt onder verschillende groeiomstandigheden te selecteren en zo te bepalen welke eigenschappen gunstig zijn voor biomassaproductie onder welke omstandigheden.

Naast een modelmatige benadering van het probleem is een experiment uitgevoerd waarin de spruit-wortel verhouding en SLA van soorten van de bosondergroei en snelgroeiende, competitatieve soorten werd vergeleken en de plastische response op standplaats-omstandigheden werd beschreven.

RESULTATEN

In hoofdstuk 3 is het plantmodel gebruikt om de hypothese te testen dat een laag specifiek bladoppervlak (eng. Specific Leaf Area, SLA) en een hoge spruit-wortel verhouding gunstige eigenschappen zijn voor soorten die zijn aangepast aan schaduwrijke omstandigheden. Hiervoor werd de biomassa-productie van modelplanten met verschillende eigenschappen onder verschillende omstandigheden geevalueerd en de eigenschappen vastgesteld waarbij maximale biomassa-productie werd bereikt. Het model liet zien dat, in overeenstemming met de hypothese, onder schaduwrijke condities planten met een lagere SLA of een hoge spruit-wortel verhouding het meeste biomassa produceerden. Een lage SLA is gecorreleerd met een lange levensduur en lage kosten voor onderhoudsrespiratie en deze strategie werd in deze studie gekarakteriseerd als een conserveringsstrategie. De rol van een lange levensduur en lage onderhoudskosten in de netto biomassa productie nam af met toenemend licht; wanneer lichtintensiteit niet meer beperkend is voor de groei van planten is conservering van verworven bouwstoffen blijikbaar minder belangrijk. De hoge spruit-wortel verhouding onder schaduwrijke omstandigheden maakte een grotere acquisitie van koolstof mogelijk en verminderde de onderhoudskosten van het (kleinere) wortelcompartiment. Bij hogere lichtbeschikbaarheid was een snellere groei mogelijk, wat een hogere vraag naar stikstof tot gevolg had en dus een verlaging van de spruit-wortel verhouding voor maximale biomassa productie.

Zoals al eerder is beschreven zijn de meeste planten zijn in zekere mate in staat hun spruit-wortel verhouding aan te passen aan de omstandigheden. In het algemeen wordt aangenomen dat plasticiteit voordelig is in habitats met gemiddeld een betere beschikbaarheid van licht en stikstof en waar een temporele variatie wordt gevonden in de beschikbaarheid van deze bouwstoffen die overeenkomt met de tijdschaal waarop de plant zich aan kan passen. Hoofdstuk 4 behandelt de vraag of plasticiteit in spruit-wortel verhouding is gunstig voor planten die zijn aangepast aan de ondergroei van loofbossen, waar de beschikbaarheid van licht in het begin van het seizoen relatief hoog is en in de loop van het seizoen afneemt.

Het model voorspelde dat in de ondergroei van loofbossen een lage plasticiteit of zelfs een rigide allocatie van biomassa gunstiger is voor biomassa productie, vooral wanneer de lage beschikbaarheid van licht gecombineerd is met een lage stikstofbeschikbaarheid. Het contrast tussen de hogere lichtbeschikbaarheid in het begin van het seizoen, en de schaduwrijke omstandigheden later in het seizoen was te groot voor de plant om een plastische aanpassing voordelig te maken. De plastische aanpassing aan de initiële hooglicht omstandigheden resulteerde in een lage spruit-wortel verhouding waardoor de plant later in het seizoen niet over voldoende spruit-biomassa beschikte om aan de koolstofbehoefte voor onderhoud en groei te voldoen. De lage lichtintensiteit resulteerde bovendien in een lagere groeisnelheid waardoor aanpassing van de spruit-wortel verhouding aan de nieuwe omstandigheden ook slechts langzaam kon verlopen.

Uit de modelsimulaties kwam dus naar voren dat een plant uit de ondergroei van een donker (loof)bos kan worden gekarakteriseerd door een lage SLA, een hoge spruit-wortel verhouding en een lage plasticiteit in spruit-wortel allocatie. Onder betere lichtomstandigheden, zoals bijvoorbeeld in de bosrand, voorspelde het model dat een hogere SLA en een hogere plasticiteit in spruit-wortel verhouding een geschikte aanpassing is. Deze modelvoorspellingen komen overeen met de experimentele resultaten gepresenteerd in hoofdstuk 5. In dit hoofdstuk werden de SLA en spruit-wortel verhouding vergeleken van vier soorten, twee typisch voor de ondergroei van (donkere) loofbossen en twee die gewoonlijk worden gevonden in de bosrand, opgekweekt onder verschillende beschikbaarheid van licht en stikstof. De twee typische bossoorten, *Circaea lutetiana* en *Mercurialis perennis*, hadden in het algemeen dikker blad en een meer rigide spruit-wortel verhouding in vergelijking met de twee bosrandsoorten, *Aegopodium podagraria* en *Impatiens parviflora*.

DE ONDERGROEI VAN BOSSEN OP VOORMALIGE LANDBOUWGROND

Op basis van de modelresultaten zijn twee soorten, een schaduwtolerante soort van de bosondergroei en een snelgroeïende, concurrentiekrachtige soort die vaker bij hoger lichtbeschikbaarheid wordt gevonden, gedefinieerd. Deze twee soorten konden vervolgens worden gebruikt om te analyseren wat er gebeurt bij verhoogde stikstofbeschikbaarheid. Hiervoor werd eerst een competitieversie van het model gemaakt waarbij de planten die hoeveelheid licht en stikstof moeten delen. Een hogere spruit of diepere worteling dan de buurplant kan hierbij een voordeel betekenen omdat daarmee een relatief grotere hoeveelheid licht of stikstof kan worden verworven dan de buurplant. De resultaten van deze simulaties zijn gepresenteerd in hoofdstuk 6.

Eerst is gekeken naar natuurlijke omstandigheden, dus lage stikstofconcentraties in de bodem. Onder deze omstandigheden en lage beschikbaarheid van licht (minder dan 10% van het licht dat boven het kronendak van het bos beschikbaar was) produceerde de bosplanten, zoals verwacht kon worden, meer biomassa dan de snelgroeïende, concurrentiekrachtige soort; bij een hogere lichtintensiteit werd het omgekeerde gevonden. Onder constante lichtomstandigheden, zoals bijvoorbeeld in naaldbossen veranderde dit patroon niet heel sterk wanneer bij een hogere beschikbaarheid van stikstof werd gesimuleerd. Onder schaduwrijke omstandigheden konden geen van beide soorten profiteren van de hogere stikstofbeschikbaarheid, bij een hogere lichtintensiteit profiteerde vooral de snelgroeïende, concurrentiekrachtige soort van het hogere stikstofaanbod.

Wanneer de lichtintensiteit niet constant was over het seizoen, zoals bijvoorbeeld in loofbossen, bleek een verhoogde stikstofconcentratie in de bodem een groter effect te hebben. Beide soorten waren in staat hun biomassaproductie te vergroten, onafhankelijk van de lichtintensiteit later in het seizoen, maar het voordeel was groter voor de snelgroeïende, concurrentiekrachtige soort dan voor de bossoort. De snelgroeïende soort

Samenvatting

was echter niet in staat om een lichtregime waarin de lichtintensiteit later in het seizoen afnam tot extreme waarden (minder dan 5% van het licht dat boven het kronendak van het bos beschikbaar was) te overleven dus alleen onder deze omstandigheden produceerde de bossoort meer biomassa dan de snelgroeïende, concurrentiekrachtige soort.

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Curriculum vitae

Marjet Elemans was born in Mierlo, The Netherlands, on May 5th 1972. After attending the Dr. Knippenbergcollege in Helmond for her secondary education she started to study Landscape Ecology and Nature Management at the IAH-Larenstein. For this study she completed three projects. Firstly, she developed a management advice of the riverbanks of the river Aa in the south of the Netherlands within the framework of the ecological policy of the Dutch (local) government. Secondly, she evaluated the methods and results of the conversion practices of coniferous forest to deciduous forest in the Dutch dune area. And, finally, she evaluated theory and practice of the management of damaged natural heather pools in the Netherlands. After graduation in 1994 she continued her studies at Wageningen University, the Netherlands, specializing in landscape ecology and plant ecology. Here she carried out two graduation projects. The first focusing on the effect of environmental factors on growth and biomass production of the mangrove species *Rhizophora* in the Mekong-Delta, Vietnam. This project consisted of a combination of field work and growth analyses. The second project involved a landscape-ecological study of the area Garderen-Uddel-Elspeet in the province of Gelderland, the Netherlands, which resulted in recommendations for future development of the area. She obtained her M. Sc. degree in November 1997.

After graduation she took up a post as consultant on ecology and vegetation science at SBW Consultancy in Wageningen, the Netherlands. In this company she was responsible for the collection of field-data and the development of management programs for several nature areas and riverbanks.

In 2000 she accepted a Ph.D. position at Utrecht University within the international research project AFFOREST. This project investigated the environmental consequences of afforestation on former agricultural land. Her research focused on the plant characteristics that play a role in the development of the forest understory. An important part of the project was the development of a mechanistic plant growth model. In 2005 she completed her Ph.D. research with the publication of this thesis.

In February 2005 she will start a post-doc project at the Iris-centre of the Karolinska Institutet in Stockholm, Sweden.

