Forest regeneration and restoration in Vietnam

View of the valley in Khe Tre

The research presented in this thesis was carried out within the framework of the Plant Ecology & Biodiversity group, Institute of Environmental Biology, Utrecht University, of Tropenbos International, Vietnam Program, and of the Prince Bernhard Chair for International Nature Conservation.

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Forest regeneration and restoration in Vietnam

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Forest regeneration and restoration in Vietnam

Regeneratie en herstel van bos in Vietnam
(met een samenvatting in het Nederlands)

Phục hồi và tái sinh rừng ở Việt Nam
(với phần tóm tắt bằng tiếng Việt Nam)

Proefschrift

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Contents

View from the road to the summit of Bach Ma (8km pole)

Chapter 1

General introduction

Tropical forests

Tropical deforestation is a major issue of international environmental concern. Tropical forests are valuable because of their high biodiversity in flora and fauna species and cultural, social and environmental functions. Nowadays, in the context of global warming, forests are also considered as important carbon sinks. Nevertheless they are disappearing at an alarmingly high rate (Hirsch 1997).

Due to the decline in primary forest area, secondary forests are becoming more important. They will increasingly provide goods and services, such as biodiversity conservation, erosion control, watershed management, soil improvement, timber production and other forest products. Everywhere in the tropics, more and more people, especially the poor, will depend on these forests to make a living. It is therefore important to increase our understanding and refine our knowledge of ecological processes involved in secondary succession (Holl and Kapelle 1999).

Secondary forest succession

Secondary forests are formed through succession: this is the alteration in structure and species composition of a vegetation stand after disturbance of the primary forest or after abandonment of agricultural fields. In essence, forest succession is the continuous replacement of tree species, starting with early pioneer (light-demanding) shrubs and trees, which are then gradually replaced by longer-lived pioneer and climax (shade-tolerant) tree species (Finegan 1984; 1996; Peña-Claros 2003). This study focuses on natural regeneration of a young secondary forest in Vietnam and on management activities that are supposed to accelerate succession.

The role of light

In wet tropical forests light seems to play a predominant role in determining the course of succession (Denslow 1987; Gilbert et al. 2001; King et al. 2005). As secondary succession proceeds both height and leaf area index of the stand increase rapidly (Swaine and Hall 1983; Uhl 1987) creating an increasingly steeper gradient in light availability. Tall plants are able to deploy their leaves in the most illuminated layers of the canopy where they can capture large amounts of light, while simultaneously shading smaller plants. It is often assumed that asymmetric competition for light, with taller plants capturing disproportionally more of the available light (Weiner 1990) and thus growing disproportionally faster, is the main factor shaping forest succession (Huston and Smith 1987; Van Breugel 2007). Taller plants will finally win the competition for light by outcompeting the smaller plants. This competition process is assumed to strongly affect the structure and species composition of the forest. The question then arises: How do morphological and physiological characteristics relate to the dominance or subordinance of secondary forest species? What are the consequences for succession?

Hirose and Werger (1995) developed an approach to relate plant size to the efficiency with which a plant uses its biomass to capture light. By dividing whole plant light capture by its above ground biomass, a measure for light capturing efficiency is obtained and the level of asymmetry in light capture can be quantified. Hirose and Werger (1995) applied this approach to grasslands and found that tall shade-intolerant plants could capture more light per unit leaf area than smaller shade-tolerant plants, simply because they occupied the more illuminated layers in the canopy. However smaller plants could capture as much or even more light per unit above ground biomass as the taller plants because smaller plants had a higher leaf area ratio (leaf area/ plant mass) than taller plants. Thus due to different morphologies, taller and smaller plants had similar light capturing efficiencies and were able to co-exist in a vegetation stand.

Similar results were obtained by Werger et al. (2002), Anten and Hirose (1999) and Aan et al. (2006) but none of these studies were done in forests. Selaya et al. (2007) applied the above mentioned approach in a young tropical regenerating forest stand and found that early and later successional species captured similar amounts of light per unit above ground biomass. These findings are in contrast to the general assumption that asymmetric light capture is important in shaping the course of secondary forest succession (Huston and Smith 1987; Van Breugel 2007).

Growth of plants does not solely depend on light capture, but also on the efficiency with which light is used for photosynthesis (LUE). Light use efficiency is highly dependent on plant physiological characteristics such as (dark) respiration, quantum yield and maximum photosynthetic rates with the latter being dependent on leaf nitrogen content and photosynthetic nitrogen-use efficiency (e.g. Anten and Hirose 2003; Ellsworth and Reich 1996; Hiremath 2000). This is the first study that relates size dependent light capture and LUE to plant growth over time on the same plants. Thus until now the degree of asymmetry of competition for light and its importance for secondary forest succession have remained unclear. It is therefore interesting to analyse the morphological and physiological processes underlying growth patterns of early successional species in a young secondary forest, and relate the efficiency of light capture and light use to the observed size hierarchy.

Nitrogen-use efficiency

During forest regeneration soil nutrient availability decreases (Ewel et al. 1991), causing species to increasingly compete for nutrients. Differences in nutrient-use efficiency between species can partly determine their competitive interactions and associated size hierarchies in plant communities (Aerts and Van der Peijl 1993). Nitrogen is an essential nutrient for plants because it is one of the main components of the photosynthetic proteins (Evans 1989). As a result of its limited availability it is one of the primary factors that limits plant growth in many natural ecosystems (Kachi and Hirose 1983; Vermeer and Berendse 1983) and it is therefore important for plants to use nitrogen efficiently. Thus a plant's nitrogen-use efficiency (NUE) may also partly determine a plant's success during succession (Ellsworth and Reich 1996; Herbert et al. 2004; van der Werf et al. 1993).

NUE can be calculated as the product of nitrogen productivity (NP: rate of dry matter production per unit of nitrogen per unit of time) and mean residence time (MRT: the amount of days that a unit of nitrogen circulates in a plant) (Berendse and Aerts 1987). In general, fast growing species reach the more illuminated layers of the canopy, which enables them to reach high values of NP (Mediavilla and Escudero 2003; Reich et al. 1999; Reich et al. 1997). Slower growing species on the other hand may have lower NP, but they have a longer MRT of nitrogen (Escudero et al. 1992; Wright et al. 2002). Consequently, there seems to be a trade-off between NP and MRT among species with different growth characteristics (Aerts 1989; Silla and Escudero 2004).

NUE consists of a suit of physiological components but it is also influenced by the plant's position in the canopy and its crown structure (i.e. leaf area distribution). Light levels decrease from the top to the bottom of the canopy and plants occupying different positions in the canopy may have very different leaf nitrogen contents and photosynthetic characteristics, and also within an individual crown nitrogen contents vary from top to bottom (Han et al. 2004; Hikosaka and Hirose 2001; Yuan et al. 2004). Much research has focused on how NP and MRT determine NUE but little work has been done to quantitatively relate the underlying mechanisms of NP and MRT to NUE (but see Funk and Vitousek 2007; Hiremath 2000).

Studies have shown that in regenerating tropical rainforest early successional species had higher potential photosynthetic nitrogen-use efficiency at the leaf-level than species that appeared later in succession (Reich et al. 1994; Selaya 2007). The question however remains how whole canopy NUE and its underlying mechanisms compare among pioneer species. I address this question here because during the first phase of succession there is generally intense competition between pioneers and small differences in nitrogen-use efficiency may partly explain the size hierarchy among species.

Retardation and acceleration of succession

Natural forest regeneration after disturbance is often slow or stagnates, many times caused by excessive growth of shrubs, grasses and herbaceous climbers that hamper tree growth and thus secondary forest succession (Aide et al. 1995; Guariguata and Dupuy 1997; Hooper et al. 2004; Lei et al. 2006; Nykvist 1996; Woods 1989). Forest succession can even be arrested for more than a decade (Bongers et al. 2002).

In recent years there has been increased attention for restoration ecology and in particular for management options to accelerate recovery of forests (Holl and Kapelle 1999; Parrotta et al.

1997). By accelerating succession more forest area is gained. This could reduce the negative impacts of world wide deforestation.

When succession is hampered by certain plant species, the growth of desirable target species should be stimulated. However, better understanding of the interaction of the target species and the surrounding vegetation is needed in order to improve the success of attempts to restore tropical forests (Hardwick et al. 2004). Forest managers need to know when, where and how to intervene to accelerate forest succession. This knowledge can be obtained by field experiments. However, experiments require a lot of time, space and money and the outcome is usually restricted to a specific set of species in a specific setting and a limited amount of experimental conditions and replicates that are created (see Paquette et al. 2006 and references therein).

Knowledge about which type of intervention to apply and when to apply it can also be obtained from well-parameterised model studies. Here I study two methods that are commonly used to accelerate succession, using such a model: liberation and enrichment planting. Liberation and planting can be approached as a geometrical problem because it is done in a three-dimensional vegetation stand with varying height and density which is opened up to a certain extent. Also the tree's crown has a three-dimensional structure and differs between species and individual trees. Therefore a three-dimensional model would be appropriate to analyse the effect of management activities on the ecological processes that determine growth of target trees. This significantly reduces the need for expensive and long-lasting experiments and strongly expands the number of settings and conditions that can be tested.

Liberation

The role of pioneer tree species in succession is important as they have the ability to overgrow grass and shrub species and in a later stage create suitable conditions for later successional species to grow (Finegan 1984; 1996). When these pioneer trees are inhibited in growth by the surrounding vegetation they can be liberated (Chapman and Chapman 1999; Dolanc et al. 2003; Fuhr et al. 2001), meaning that the surrounding vegetation around target plants is removed. Liberation reduces competition with neighboring vegetation for below ground resources and light and thus facilitates a more rapid succession. Similarly in a later stage, later successional species can be liberated.

Species have very different light requirements (Ådjers et al. 1995; Dupuy and Chazdon 2006; Ramos and del Amo 1992). Some plants may grow best under full daylight while others require optimal light levels for growth that can be as low as 10-20% of full daylight. Pioneer species require more light than later successional species. Also over the life of a plant light requirements may differ (Davidson et al. 2002): seedlings and saplings often require more shade than adult trees. Thus the light levels created by liberation may be suitable for some plants but not for others (Dupuy and Chazdon 2006; Montagnini et al. 1997; Ramos and del Amo 1992). As a result, liberation has not always had the desired effect (Chapman et al. 2002). With a well-parameterised mechanistic growth model the effects of liberation activities can be studied.

In South East Asia species of the shrub *Melastoma* grow excessively on degraded lands (Davies and Semui 2006). Species of the family Melastomataceae often grow on degraded lands and are known to inhibit succession (DeWalt 2003). Pioneer tree species of the genera *Mallotus* and *Macaranga* regenerate on deforested or degraded lands (Lee et al. 2005; Slik et al. 2003; Toma et al. 2005) and are characteristic of secondary forests in South-East Asia (Primack and Lee 1991; Steenis 1965). These early successional species are important because they have the potential ability to overgrow *Melastoma* and thus facilitate succession. It is therefore important to determine if these tree species are limited in growth by the surrounding vegetation (that consists largely of *Melastoma* shrubs) and if liberation would result in these species having faster growth. In this dissertation I study this in a field experiment and in a modeling approach.

Enrichment planting

Another method to accelerate or supplement succession is the planting of ecologically or economically valuable tree species in an artificially created (timber) plantation or in the understory of a young forest. This is called enrichment planting.

In South East Asia large areas of (secondary) forest are converted into grasslands dominated by *Imperata cylindrica* (Otsamo et al. 1997; Werger 1983). These grasslands are difficult to reforest because of fierce competition of the grasses, fire susceptibility and soil degradation. Thus the original rain forest tree species may not be appropriate for first rotation reforestation of grasslands.

I. cylindrica is an aggressive weed but intolerant to shade. Therefore for forest plantation on such lands to be successful it is necessary to quickly create a closed canopy in order to eliminate the grass. Often exotic species are used for this purpose, such as *Acacia* species (McNamara et al. 2006; Otsamo et al. 1997). After a canopy has been created and grasses are suppressed, species native to the area can be planted under the canopy. Overstory thinning is often applied to create favorable light levels for the underplanted trees (McNamara et al. 2006; Otsamo 1998).

Not only plantations are suitable for enrichment planting. Native species are also often planted in naturally existing regenerating vegetation in order to accelerate or supplement forest succession. The most generally used method for enrichment planting in natural vegetation is line planting. Lines of a certain width are created in the existing vegetation in which native species are planted. This method has several advantages with respect to planting under a canopy of exotic trees. No clear-cutting or pre-planting with fast growing exotics is needed and species that would fail under open-site conditions can be planted.

As mentioned, species have different light requirements thus light levels at which species are planted affect them differently in terms of survival and growth. Studies that have shown interspecific variation in growth between underplanted tree species in relation to different overstory densities stress the importance of species and site selection and suggest further studies on species-site matching (Ådjers et al. 1995; Lof et al. 2007; McNamara et al. 2006; Montagnini et al. 1997; Otsamo 1998). Here I study the photosynthetic rates of species planted in two different secondary forest stands and, using the modeling approach, determine the effects of line width, height and density of the vegetation on species with different morphological and physiological traits.

Objectives of this study

Even though the importance of secondary forests has become clear recently, there is still little ecological understanding of underlying processes steering natural succession in these forests, especially in very early stages when competition is mainly between early successional species. Also little is known about the interaction of species with its surrounding vegetation, whether these species are naturally occurring or planted. The aims of this dissertation are therefore:

1) to study the morphological and physiological traits related to light competition and nitrogen-use efficiency of competing early successional species
2) to evaluate how competition for light and nitrogen-use efficiency relate to the size hierarchy of species in the early stages of succession
3) to quantitatively examine the effect of different management practices on naturally occurring and planted target trees

Outline of the dissertation

The morphological and physiological traits that are related to light competition and nitrogen-use efficiency and that determine the observed size hierarchy of early successional species during the first 5 years of succession, have been studied with a mechanistic approach. Different management activities aimed at accelerating secondary forest succession were studied with a combination of field studies, experiments and modeling.

Chapter 2 describes how the degree of size-asymmetric competition for light and light use efficiency determine growth of tree species and a woody shrub during the very early stages of succession. Individual plants were followed in time and the observed size hierarchy was related to light capture per unit above ground mass.

Chapter 3 focuses on which morphological and physiological traits determine whole canopy nitrogen-use efficiency and to what extent, how this relates to the size hierarchy among competing pioneer species and how this changes in time.

Chapter 4 presents the outcome of a liberation experiment that was done on pioneer trees in a young secondary forest. A model was used which made it possible to determine the effect of liberation in different scenarios, i.e. with increasing gap radius and in different successional stages of the same vegetation stand.

Chapter 5 determines the photosynthetic rate of target species planted in two different secondary forest stands. The effects of planting in different successional stages of a stand, with different line

width and the effect of overstory thinning were analysed by explaining the morphological and physiological traits that influence plant growth.
Finally the results are summarised and discussed.

Vietnam

In relative terms, forest loss is most serious in South East Asia. Direct causes of forest loss and degradation include unsustainable large-scale logging and the subsequent encroachment of shifting cultivation into the remaining forest areas.

This study was done in Vietnam. The total forest cover in Vietnam declined rapidly from around 43% of the country's surface area in the 1940s to 17% by the late 1970s (De Koninck 1999). During the second Indochina war (1965-1975) the country lost large areas of forest due to the destructive effects of bombs and Agent Orange, a defoliating chemical that was sprayed from aircrafts and leached into the soil. The destroyed areas are often being invaded by fire-prone grasses and vines which may arrest succession by preventing the establishment and growth of tree species (Orians and Pfeiffer 1970). Since the war even larger areas have been cleared due to logging activities, both for domestic use and as an export industry, shifting cultivation, agricultural activities (slash and burn), the establishment of timber plantations and infrastructural developments due to an increasing human population pressure (Hirsch 1997).

In 1988 the government of Vietnam launched the 5 Million Hectare Reforestation Program (5MHRP) (1998-2010). The goal is to increase forest cover to the level it used to be in the 1940s by enrichment planting, reforestation, protection and the establishment of natural reserves (MARD 2001). The forest cover has increased since then but the quality of the forest is still poor. Timber volume is low and valuable species are lacking as a result of overexploitation.

Study site

Part of this study was done in Bach Ma National Park (16°10'N 107°50'E) (Fig. 1) and part in its bufferzone close to the village of Khe Tre. The park is located in Thua Thien Hue province in central Vietnam. It is situated on a ridge towards the southern end of the Annamite mountains and forms a biogeographic boundary between the floras and the faunas of northern and southern Vietnam. It is probably the wettest place in the country with up to 8 m of rain annually on the top of Bach Ma mountain (1450 m above sea level).

The main forest types found within the park are lowland evergreen forest below 900 m and montane evergreen forest above. Large areas of the forest were destroyed by defoliants and bombs during the second Indochina war. Subsequent large-scale commercial logging practices resulted in the decline of economically valuable trees. Illegal exploitation of timber and non-timber forest products has continued after the cessation of official logging operations. As a result of these activities, no undisturbed forest now remains in the park. There are large parts covered by shrubs and grasses which hardly regenerate due to periodic burning. Aforestation and reforestation are key activities of the park scientific staff.

Fig. 1 Location of Bach Ma National Park (source: www.bachma.vnn.vn)

Tropenbos International

The fieldwork of this study took place within the framework of Tropenbos International (TBI). TBI is a Dutch NGO which aims to contribute to the conservation and sustainable use of tropical rain forests by providing relevant knowledge, deepening insight and developing and testing methods that can be used at policy and management levels. In order to achieve this goal, TBI tries to ensure that research results are reflected in legislation and regulatory measures and are applied in planning and management.

The TBI-Vietnam Program was implemented in 2002. Besides contributing to the conservation and sustainable use of tropical forest resources, the aim is also to strengthen Vietnam’s professional and institutional capacity. TBI-Vietnam aims to generate and disseminate meaningful information, promote its transfer into policy and the practice of forest management and provide education and trainings to university students and other organisations. The 5MHRP partly forms TBI-Vietnam’s framework for action.


Start of regeneration (behind is a 5 year old forest)


Competing tree and shrub (0.5 year old stand)

Chapter 2

The limited importance of size-asymmetric light competition and growth of pioneer species in early secondary forest succession

with N.P.R. Anten, R.J. Oomen, D.W. van Bentum and M.J.A. Werger

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Abstract

It is generally believed that asymmetric competition for light plays a predominant role in determining the course of succession by increasing size inequalities between plants. Size-related growth is the product of size-related light capture and light use efficiency (LUE). A canopy model was used to calculate light capture and photosynthetic rates of pioneer species in sequential vegetation stages of a young secondary forest stand. Growth of the same saplings was followed in time as succession proceeded. Photosynthetic rate per unit plant mass (P_{mass}: mol C $g^{-1}day^{-1}$), a proxy for plant growth, was calculated as the product of light capture efficiency (Φ_{mass}: mol PPFD $g^{-1}day^{-1}$) and LUE (mol C mol $PPFD^{-1}$). Species showed different morphologies and photosynthetic characteristics but their light capturing efficiencies and light use efficiencies, and thus P_{mass}, did not differ much. This was also observed in the field: plant growth was not size-asymmetric. The size hierarchy that was present from the very early beginning of succession remained for at least the first five years. Thus in a slow growing regenerating vegetation the importance of asymmetric competition for light and growth can be much less than often assumed.

Introduction

Secondary forest succession is generally described as the process in which different (groups of) species replace each other in time after a disturbance (Finegan 1984; Peña-Claros 2003). Natural forest regeneration after disturbance is often slow or stagnates, many times caused by excessive growth of shrubs or grasses (e.g. Aide et al. 1995; Guariguata and Dupuy 1997; Nykvist 1996).

In wet tropical forests light seems to play a predominant role in determining the course of succession (Denslow 1987; Gilbert et al. 2001; King et al. 2005). As secondary succession proceeds both height and leaf area index of the stand increase rapidly (Swaine and Hall 1983; Uhl 1987) creating an increasingly steeper gradient in Photosynthetic Photon Flux Density (PPFD, 400-700 nm) and plants therefore strongly compete for light.

Competition for resources can be either symmetric or asymmetric and the degree of asymmetry can have profound consequences for the dynamics in vegetation stands (Weiner 1990; Weiner and Thomas 1986). In the case of symmetric competition individuals grow in proportion to their size while under asymmetric competition larger individuals grow disproportionately faster. The latter results in increased size inequality among plants (Weiner 1990). It is often assumed that competition for light is asymmetric since larger individuals shade smaller ones but not vice versa (Ford 1975; Schwinning and Weiner 1998). This in turn has lead to the connotation that asymmetric competition for light is the main force shaping secondary succession in tropical forests (Huston and Smith 1987; Van Breugel 2007).

Growth relative to size can be calculated as the product of size-dependent light capture and light use efficiency (Hikosaka et al. 1999; Schwinning 1996; Schwinning and Weiner 1998). Hirose and Werger (1995) introduced a model approach by which interspecific differences in light capture of grasses and herbs were related to differences in size: i.e. leaf area and aboveground mass. Shorter subordinate species captured similar amounts of light per unit aboveground mass (Φ_{mass}) as taller ones despite the fact that they were growing in the shade (see also Aan et al. 2006; Anten and Hirose 1999; Hirose and Werger 1995). Going by the definition of Schwinning and Weiner (1998) this similarity in Φ_{mass} indicates that, contrary to what is generally assumed, light competition among these species was size-symmetric (Anten and Hirose 1998). Light use efficiency is highly dependent on plant physiological characteristics such as (dark) respiration, quantum yield and maximum photosynthetic rates with the latter being dependent on leaf nitrogen content and photosynthetic nitrogen-use efficiency (e.g. Anten and Hirose 2003; Ellsworth and Reich 1996; Hiremath 2000).

As far as we know only one study (Selaya 2007) has quantified light capture and photosynthesis of individual plants in a secondary tropical forest. She found that the two disproportionately fastest growing species achieved high photosynthetic rates not due to higher light capturing efficiencies but due to high light use efficiencies. But in secondary tropical forests no one so far has related size dependent light capture and LUE to plant growth over time on the same plants. Thus the degree of asymmetry of competition for light and its importance for secondary forest succession remain unclear.

Here we quantify light competition, light use, photosynthetic rates and growth of early successional species in central Vietnam. Traditionally Vietnam is a forested country but it has lost many of its forests due to wars, fires, logging and agricultural practices (Blanc et al. 2000; Chien 2006; Hirsch 1997) and natural forest regeneration is slow (Orians and Pfeiffer 1970). Most field studies on succession have been done in chrono-sequences, in which sites of different age are studied simultaneously (Selaya et al. 2007; Werger et al. 2002). Such studies have many assumptions regarding site history, environmental conditions and seed availability (Bakker et al. 1996; Chazdon et al. 2007). Here we follow the same individuals in time during the first 18 months of secondary succession. A slightly older vegetation stand with higher LAI and vegetation height was studied as well. Observed above ground growth patterns of early successional species and the underlying processes concerning light capture (morphology) and light use efficiency (physiology), will be analysed with a mechanistic approach.

Methods

Study area

The study site is located in the buffer zone of Bach Ma National Park, Thua Thien Hue Province, in central Vietnam (16°10’N 107°50’E). Bach Ma National Park and its buffer zone were established in 1991 with a total area of 43,331 ha. It is the core of the last remaining contiguous forest belt in Vietnam, stretching from the South China Sea to the border with Laos. The area experiences high rainfall, especially from November until February (up to 8,000 mm per year on top of Bach Ma mountain). There is no distinct dry season and the vegetation is evergreen (Tran and Ziegler 2001). After defoliation and destruction in the war (1965-1975), the study site was used for monoculture plantations of *Acacia mangium*. Part of the site (two hectare) was left fallow in 1999 and was a 5-year-old (5 y/o) secondary forest stand at the start of this study.

Species selection

We selected four study species in 2004, all co-dominant in the stand: the shrub, *Melastoma candidum* (Melastomataceae) and three tree species, *Mallotus microcarpus*, *Mallotus paniculatus* and *Macaranga denticulata* (all Euphorbiaceae). They represented over 75% of the total plant cover and were the only woody species present in sufficient numbers for study. Species of *Melastoma* (Davies and Semui 2006), *Mallotus* and *Macaranga* (Lee et al. 2005; Slik et al. 2003; Toma et al. 2005) are known to regenerate on deforested or degraded lands and are characteristic of secondary forests in South-East Asia (Primack and Lee 1991; Steenis 1965).

We selected plants for inclusion in this study from a 2 ha area making sure they covered the entire height range (up to 8 m high). Selected individuals were surrounded by other saplings of the same species and by other secondary vegetation such as ferns (*Dicranopteris linearis*), grasses (*Phragmites communis, Imperata cylindrica*) and lianas. Together these groups were estimated to contribute less than 25% to the total leaf area of the stand. Later successional species were absent at this stage. It can thus be assumed that competition was mostly among the four selected species.

Measurements

Measurements on the individuals in the 5 y/o stand (vegetation stage IV) were done in September and October of 2004. Light climate, LAI and biomass allocation were determined per individual so that light capture could be calculated. In November 2004 the area was experimentally slashed and burned. After 150 days (spring 2005; vegetation stage I) 50 individuals per species divided over 10 plots of 25m^2 each, were randomly selected and measured non-destructively (light climate, LAI and biomass allocation). The same saplings were measured again at 330 days (fall 2005; vegetation stage II) and 510 days (spring 2006; vegetation stage III) after the slash and burn treatment. More than one third of the saplings died during the course of the study due to anthropogenic factors but care was taken that all individuals included in the data analysis were not disturbed. We analysed data in two ways: using all individuals present at a certain time and using only individuals that survived until stage III. As results were very comparable, we chose to include all individuals for the analyses, except for growth analysis that was done for surviving individuals only.

In vegetation stage IV we established plots of 9m^2 each containing an individual sapling in the center, in which light and LAI was measured. Within the 25m^2 plots of vegetation stage I,II and III we created 1m^2 subplots to measure light and LAI. All measurements were done similarly in all vegetation stages, under a uniform overcast sky. Photosynthetic Photon Flux Density (PPFD, 400-700 nm) was measured in the center of each quadrant of each (sub)plot, summing up to four light profiles per target individual. These were averaged per (sub)plot. Light was measured at ground level, 0.25 m, 0.5 m, 0.75 m and 1 m using spherical light quantum sensors and meters (LI-250, LiCor). Field testing revealed that light levels higher up in the canopy could be accurately calculated from these values. Simultaneously light measurements were done above the vegetation canopy. The Leaf Area Index (LAI) was measured four times in each (sub)plot at ground level from every corner of the (sub)plot facing the center (LAI-2000 Plant Canopy Analyzer, LiCor, NE, USA). Vertical leaf area distribution was determined by counting the number and recording the height of leaves touched by a telescopic rod when moved up through the vegetation. This was done in the center of each quadrant of a sub(plot).

For individuals in vegetation stage IV height up to the highest leaf was recorded. Leaf angles of 20 leaves randomly distributed over the tree’s crown were measured for 6 individuals per species. The sapling was harvested: leaves were collected per layer of 25 cm whereas stem, branches and petioles were pooled for the whole sapling. Leaf area was measured with a digital photograph (SigmaScan Pro 5.0). All samples were dried in an oven for 72 hours at 70°C and weighed. Nitrogen content of the leaves was analysed with a continuous flow analyzer (SKALAR, Breda, the Netherlands) following the Kjeldahl method.

In vegetation stages I, II and III we measured the following parameters on saplings: height, leaf angles, length and diameter of stem, branches and petioles and length and width of leaves. To obtain allometric relations between dimensions and biomass of above ground plant parts, 20 individuals per species were harvested in the same height range as the studied individuals. The same dimensions were measured and dry weight of stem, braches, petioles and leaves was determined. Dry weights and estimates based on dimensions were correlated and the function that best described dry weight (r^2 varied from 0.92 to 0.99) was used to calculate dry weight of studied saplings.

In March 2005, photosynthesis measurements were done using an open gas exchange system (CIRAS 2, PP systems, Hitchin, UK) equipped with a LED light source. Up to 28 leaves of varying age (young, medium and old: related to position on the branch) were selected on different individuals (max. three leaves per individual) that were growing outside the plots. Photosynthetic rates were measured early in the morning when stomata were open. Maximum photosynthetic rates were measured at Photosynthetic Active Radiation (PAR) values of 1200-1500 μmol $m^{-2}s^{-1}$. In order to determine dark respiration and quantum yield we varied light from 80 to 0 μmol $m^{-2}s^{-1}$ PAR in steps of 10-20 μmol $m^{-2}s^{-1}$. The CO_2 concentration in the chamber was maintained at 370 ppm throughout all measurements.

Model description

The model used here is almost identical to the one used by Anten and Hirose (2003) and was described into detail by them. Here a short description is given including references to equations used by them. The model simulates plots as used by us (1m^2 in vegetation stages I-III and 9m^2 in IV) with 25 cm horizontal vegetation layers. In each layer the leaf area of target individuals and neighbors are assumed to be randomly distributed. Instantaneous photosynthesis is calculated as a function of leaf nitrogen content and absorbed photon flux, which in turn is a function of the leaf angle distribution and leaf absorbance of a target individual and the surrounding vegetation. With respect to light capture two classes of leaves are distinguished: shaded and sunlit (following De Pury and Farquhar 1997). The photon flux captured by the shaded leaf area is calculated by summing the diffuse sky irradiance and the scattered beam irradiance (eq.(1)-(5) in Anten and Hirose 2003). Sunlit leaves receive direct beam and diffuse sky irradiance (eq.(6)-(7) in Anten and Hirose 2003). Since the distribution of diffuse irradiance is incident under various angles, the sky dome is divided into three zones from which diffuse irradiance is calculated assuming a standard overcast sky (Goudriaan 1977). For the calculation of the extinction coefficient for light three leaf inclination classes are assumed following Goudriaan (1988) (see eq.(3)-(6) in Anten 1997). The distribution of diffuse light thus calculated corresponded well with our measured light gradients.

A non-rectangular hyperbola was used to characterise the light response of net leaf photosynthesis (Johnson and Thornley 1984) (eq.(8) in Anten and Hirose 2003). Light saturated rates of photosynthesis are linearly dependent on leaf nitrogen content per unit leaf area (eq.(9a) in Anten and Hirose 2003) but dark respiration is assumed to be constant in our study. For the quantum yield we used the measured value and the curvature factor was set to 0.8 (Hirose et al. 1997).

Calculation of the distribution of light saturated photosynthetic rates in the sapling's crown was done as a function of the nitrogen (N) distribution (Hirose and Werger 1987). Here the calculation deviates from Anten and Hirose (2003). N content was only measured in the most illuminated leaves (2-3) in the top of the crown (N_o) in vegetation stage III. We calculated the N distribution in the crown (N_{area}) using the equation proposed by Anten (1997): $N_{area}=N_o(I/I_o)^{0.4}$ with I/I_o the relative light intensity. This equation shows that the N distribution scales with the light distribution by a power 0.4. This is based on the mean distribution of N in various stands reviewed by Anten (1997). For stages I and II no direct N measurements were done. N content of young fully exposed leaves in the top layer of the crown of an individual in these stages was assumed to be similar to the N content as in stage III, corrected for the SLA of the fully exposed leaves. N content further below in the canopy was calculated similarly as before.

Whole plant carbon gain was calculated by integrating leaf photosynthesis over canopy depth for each layer separately and distinguishing between photosynthesis of shaded and sunlit leaves. Next, these values were integrated over all layers of the plant (eq.(10)-(11) in Anten and Hirose 2003) and over the entire day to obtain the daily photosynthetic rate at plant level (from sunrise to sunset at the latitude of the study site on the median day of the measurements) (cf. Gates 1980). Whole plant daily light capture was calculated similarly.

Photosynthetic rate per unit above ground mass (P_{mass}: mol C $g^{-1}day^{-1}$) was calculated by dividing whole plant daily photosynthesis by the above ground plant mass. P_{mass} consists of two components; Φ_{mass} and Light Use Efficiency (LUE).

$$P_{mass}= \Phi_{mass}*LUE \qquad (1)$$

where Φ_{mass} is the daily light capture per unit above ground mass (mol PPFD $g^{-1}day^{-1}$) and LUE is photosynthesis per unit of absorbed light (mol C mol $PPFD^{-1}$).

Dividing whole plant daily light capture by the above ground mass also gives Φ_{mass} and by dividing daily light capture by leaf area we obtain Φ_{area}, following Hirose and Werger (1995). In turn, Φ_{mass} is equal to the product of Φ_{area} and LAR:

$$\Phi_{mass}= \Phi_{area}*LAR \qquad (2)$$

where Φ_{area} is the daily light capture per leaf area (mol PPFD $m^{-2}day^{-1}$) and LAR is the Leaf Area Ratio ($m^2 g^{-1}$).
LAR is made up of two components: Specific Leaf Area ($m^2 g^{-1}$) and Leaf Mass Ratio ($g\ g^{-1}$):

$$LAR=SLA*LMR \qquad (3)$$

Note that in this study LAR and LMR are calculated on the basis of above ground biomass.

Statistical analyses

Data of saplings in vegetation stage IV were (log)transformed when necessary, after Levene's test. The effect of species on the average values of height, plant mass, SLA, LMR, LAR, Φ_{area}, Φ_{mass}, LUE and P_{mass} were analyzed using ANOVA tests, with Bonferroni (equal variances assumed) or Games-Howell (equal variances not assumed) post-hoc tests to test for differences among species. To test for slope-effects in the relations between SLA, LMR, LAR, Φ_{area} and Φ_{mass} and individual height we used ANCOVA.

We created plots after the slash and burn treatment to trace back the saplings in the following measuring period. However, in this set-up both plot-effects and individuals-effects might occur. Therefore analyses of the saplings were done with Linear Mixed Effects Model (in results section abbreviated as MM). Whenever values of variables were analysed within one measuring period, plot number was identified as subject. The effect of species on the average values of RGR (of above ground biomass), height, plant mass, SLA, LMR, LAR, Φ_{area}, Φ_{mass}, LUE and P_{mass} was determined by identifying these variables as dependent and species as factor. When designing the model, species was the sole fixed effect, including intercept. For random effect an intercept was included for the subject plot number, but no model for random effects was designed. No post-hoc tests were available but most between-species differences could be deduced from the parameter estimates. When the change in the variables between species were analysed with time or height, subjects included plot number and individual number. The variable on the y-axis was the dependent, the variable on the x-axis the covariate (time or height) and species was the factor. Slope-effects were tested by designing a model with an interaction term of the fixed effects 'species' and 'time' or 'height'. If a significant slope-effect was absent ($P>0.05$), the test was repeated with both fixed effects as main effects. For random effect an intercept was included for the subjects 'plot number' and 'individual number', but no model for random effects was designed.

Average values of the photosynthetic characteristics were analysed using ANOVA tests with Bonferroni post hoc tests. The increase in photosynthetic rates with light (quantum yield) and the slopes of the P_{max}-N_{area} relation were analysed with an ANCOVA test.

Results

Canopy characteristics

Light and Leaf Area Index (LAI) distribution in the canopy of each vegetation stage is given in Fig. 1a-d. In vegetation stages I, II and III the LAI tended to be concentrated near the soil while in stage IV it was more evenly distributed throughout the vegetation.

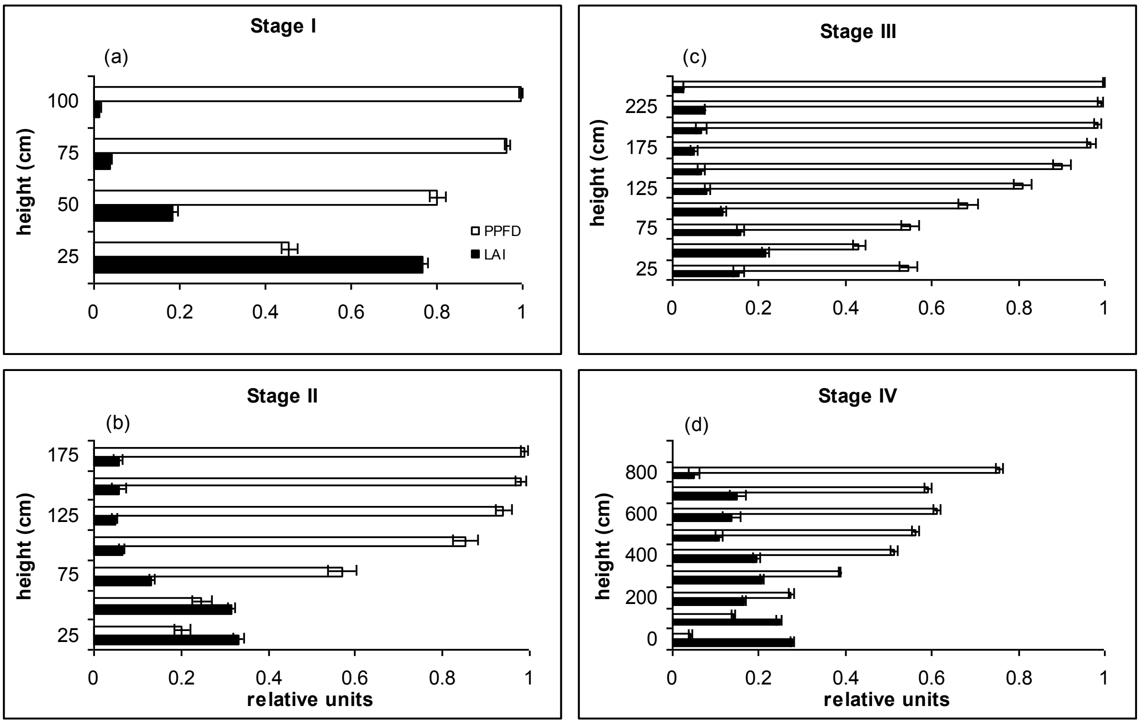

Fig. 1a-d Light (PPFD) and LAI distribution in the canopy of four successional secondary forest stages. Stage I, II and III are stages of the same stand. Stage IV is a separate stand. Note that in stage IV layers of 25 cm are grouped together into layers of 1 m. Bars denote standard error.

Sapling growth

In vegetation stages I, II and III *Mallotus microcarpus* attained the greatest height (Fig. 2a) (MM, $p<0.001$) and it exhibited the fastest increase in height with time (MM, $p=0.003$). Its above ground plant mass was also higher than the mass of the other species at all vegetation stages (Fig. 2b) (MM, $p<0.001$). *Melastoma candidum*, i.e. the smallest species, exhibited the highest RGR in the period from 150 until 510 days after the slash and burn treatment (Fig. 3) (MM, $p<0.001$) (note that RGR was solely calculated for above ground biomass). Consequently, size inequalities that were present 6 months after the slash and burn treatment decreased somewhat during the subsequent year. Within species there was no relation between RGR and individual plant height (MM, $p>0.05$). RGR was also calculated for half year periods (results not shown) but values did not significantly differ from the RGR values calculated over a year.

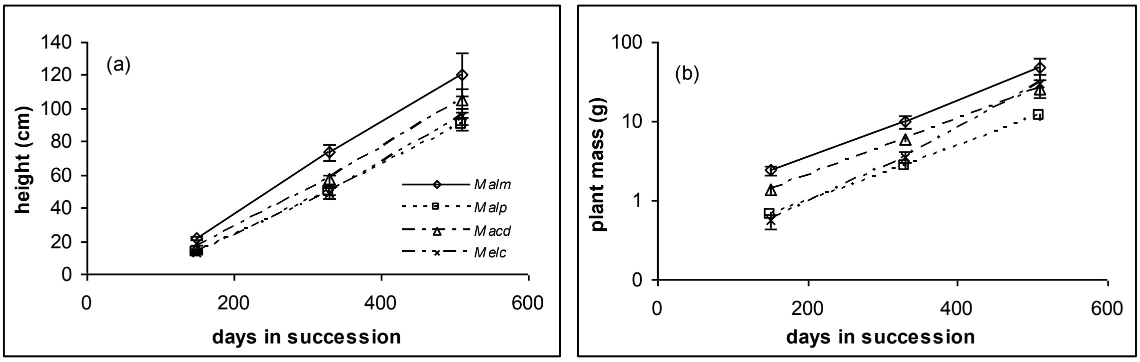

Fig. 2a-b Height (a) and above ground plant mass (b) of pioneers species during early forest succession in Vietnam (150-510 days after the slash and burn treatment). Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata; Melc, Melastoma candidum*. Bars denote standard error**.**

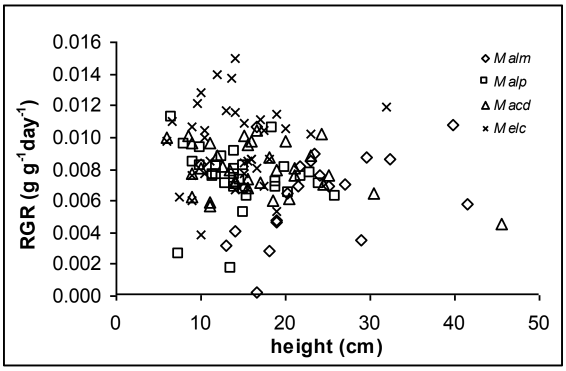

Fig. 3 Relation between above ground Relative Growth Rate (RGR) and height for four pioneers species calculated for a 360 day period from 150-510 days after the slash and burn treatment. Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata; Melc, Melastoma candidum*.

Interspecific differences in photosynthetic rates, light capture and use and biomass allocation

Photosynthesis per unit above ground mass (P_{mass}) was calculated as the product of a physiological component, Light Use Efficiency (LUE), and a morphological component, light capture per unit above ground mass ($\Phi_{mass,}$ calculated with the model) (eq.(1)). Fig. 4a-c show how these components varied in time and how they determined P_{mass} from 150-510 days in succession. The greater LAI in stage II as compared to stages I and III (Table 1), were not reflected in greater differences between species in Φ_{mass} or P_{mass}, indicating that there was no effect of these differences in LAI on interspecific competition (regardless of species height).

Table 1 Characteristics of successional vegetation stages of a Vietnamese forest

	Stage I	Stage II	Stage III	Stage IV
age (days)	150	330	510	5 years
mean LAI (m^2m^{-2})	3.03+/-1.74	5.46+/-0.91	3.73+/-0.75	5.72+/-1.16
mean height (m)	0.61+/-0.18	0.99+/-0.31	1.4+/-0.41	4.71+/-1.54

Note: stages I,II and III are different successional stages of one stand

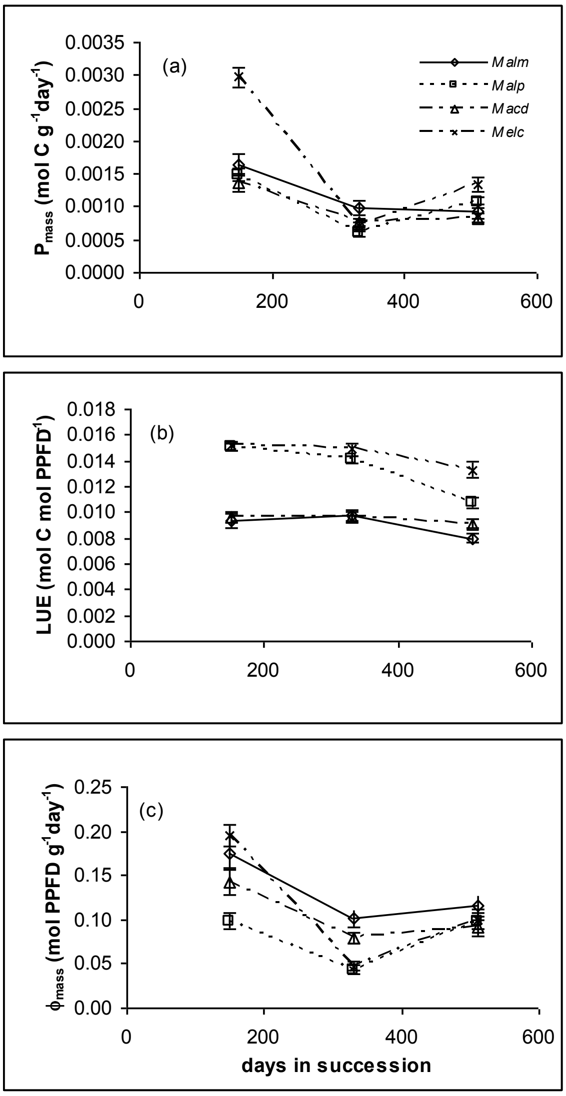

Fig. 4a-c P_{mass}, LUE and Φ_{mass} of saplings during forest succession (150-510 days after the slash and burn treatment). Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata; Melc, Melastoma candidum*. Bars denote standard error.

Melastoma candidum exhibited higher average P_{mass} values on average than *Mallotus paniculatus* and *Macaranga denticulata* (Fig. 4a) (MM, p=0.003) but not higher than *Mallotus microcarpus*. The interspecific differences could not be related to species height. LUE was higher for *Mallotus paniculatus* and *Melastoma candidum* than for the other two species (Fig. 4b) (MM, p<0.001). This can be explained by the photosynthetic characteristics of the two species (Table 2): both had low dark respiration. Quantum yield, maximum photosynthetic rate (P_{max}) and photosynthetic nitrogen use efficiency (PNUE) were similar for all species. The differences in Φ_{mass} between species were not very large (Fig. 4c). Even though *Mallotus microcarpus* showed the highest Φ_{mass} on average (MM, p<0.001), there was no relation between species height and Φ_{mass} which indicated that the degree of asymmetric competition for light was small. Φ_{mass} equals the product of Φ_{area} (calculated with the model) and LAR (eq.(2)). *Mallotus microcarpus* had a higher Φ_{area} on average than the other species (MM, p=0.009) but a similar LAR (Table 3). The small differences in Φ_{mass} were caused by small differences in LAR between species which in turn were caused by differences in SLA (Table 3) (eq.(3)) with *Mallotus microcarpus* and *Macaranga denticulata* having relatively high SLA values (but see below).

Table 2 Photosynthetic characteristics of pioneer species: quantum yield, light compensation point, dark respiration, maximum photosynthetic rate (P_{max}) and photosynthetic nitrogen-use efficiency (PNUE)

Species	n	quantum yield (μmol C $PPFD^{-1}$)	s.e.	light compensation point (PPFD)	s.e.	dark respiration (μmol $m^{-2}s^{-1}$)	s.e.	P_{max} (μmol $m^{-2}s^{-1}$)	s.e.	PNUE (μmol C mmol $N^{-1}s^{-1}$)	s.e.
Mallotus microcarpus	15-23	0.03^{a}	0.00	46.0^{a}	8.4	1.0^{a}	0.2	12.8^{a}	1.3	0.125^{a}	0.011
Mallotus paniculatus	15-28	0.03^{a}	0.00	7.4^{b}	2.0	0.2^{b}	0.1	8.6^{a}	0.7	0.104^{a}	0.007
Macaranga denticulata	16-17	0.04^{a}	0.00	15.5^{bc}	3.5	0.5^{c}	0.1	9.8^{a}	1.4	0.122^{a}	0.014
Melastoma candidum	10-16	0.04^{a}	0.00	22.5^{c}	2.9	0.4^{bc}	0.0	10.8^{a}	1.1	0.138^{a}	0.009

Notes: Values are means. Significance for species-effect (ANOVA) is indicated with different superscript letters (Bonferroni post hoc test, $p<0.05$). Letter n indicates sample size (# leaves) and s.e. indicates standard error of the mean

Table 3 Specific Leaf Area **(**SLA), Leaf Mass Ratio (LMR), Leaf Area Ratio (LAR) and light capture per unit leaf area (ϕ_{area}) of pioneer species in successional vegetation stages

Stage	Species	n	SLA (m^{2}g^{-1})	s.e.	p-value	LMR (g g^{-1})	s.e.	p-value	LAR (m^{2}g^{-1})	s.e.	p-value	ϕ_{area} (mol m^{-2}day^{-1})	s.e.	p-value
I	*Mallotus microcarpus*	50	0.0167	0.000		0.716	0.010		0.0119	0.000		14.26	2.29	
	Mallotus paniculatus	50	0.0092	0.000		0.784	0.010		0.0071	0.000		13.81	1.99	
	Macaranga denticulata	50	0.0162	0.000		0.643	0.013		0.0104	0.000		12.98	1.67	
	Melastoma candidum	50	0.0128	0.000		0.774	0.008		0.0099	0.000		19.43	1.67	
	species effect				0.000			0.000			0.000			0.033
II	*Mallotus microcarpus*	46	0.0167	0.000		0.336	0.011		0.0056	0.000		18.46	1.74	
	Mallotus paniculatus	43	0.0103	0.000		0.480	0.014		0.0049	0.000		8.70	0.92	
	Macaranga denticulata	49	0.0159	0.000		0.431	0.012		0.0068	0.000		12.18	1.21	
	Melastoma candidum	43	0.0130	0.000		0.465	0.014		0.0060	0.000		8.13	0.92	
	species effect				0.000			0.000			0.000			0.000
III	*Mallotus microcarpus*	22	0.0163	0.000		0.329	0.026		0.0053	0.000		21.41	1.86	
	Mallotus paniculatus	32	0.0134	0.000		0.360	0.014		0.0048	0.000		20.37	1.59	
	Macaranga denticulata	34	0.0155	0.000		0.278	0.016		0.0043	0.000		21.18	1.55	
	Melastoma candidum	35	0.0133	0.000		0.395	0.019		0.0052	0.000		18.55	1.82	
	species effect				0.000			0.000			0.039			n.s.
Mean for stage I, II and III	*Mallotus microcarpus*		0.0166			0.460			0.0076			18.04		
	Mallotus paniculatus		0.0110			0.542			0.0056			14.29		
	Macaranga denticulata		0.0159			0.451			0.0072			15.45		
	Melastoma candidum		0.0130			0.545			0.0071			15.37		

Notes: Values are means. Significance levels (p-values) of the overall species-effect (Linear Mixed Effect Model) are shown per stage (n.s. indicates a p-value greater than 0.05). Letter n indicates sample size and s.e. indicates standard error of the mean

Because of the higher LAI and a more than three-fold greater vegetation height, one would expect stronger competition between species in stage IV than in the younger stages. P_{mass} differed between species (Fig. 5a). *Mallotus microcarpus* had the same value as *Melastoma candidum* and these were lower than the values of *Mallotus paniculatus* and *Macaranga denticulata* (ANOVA, p=0.006). There was no clear relation between species height and P_{mass}. LUE was highest for *Melastoma candidum* (Fig. 5b) (ANOVA, p<0.001). There were differences in the Φ_{mass} values (Fig. 5c) (ANOVA, p=0.004) with the tallest and the smallest species having similar, relatively low Φ_{mass} compared to the species with intermediate height. Values of Φ_{mass} were 10-fold lower than in the younger stages because plants had lower LAR and Φ_{area} (Table 4). Values of Φ_{area} were on average the same for all species in stage IV (Table 4) (ANOVA, p=0.558), so between species differences in Φ_{mass} were caused by differences in biomass allocation (Table 4) (eq.(2)). *Mallotus microcarpus* had a relatively low LMR which caused a low LAR while *Mallotus paniculatus* had a high SLA and thus a high LAR (eq.(3)). *Macaranga denticulata* and *Melastoma candidum* had intermediate values for LAR.

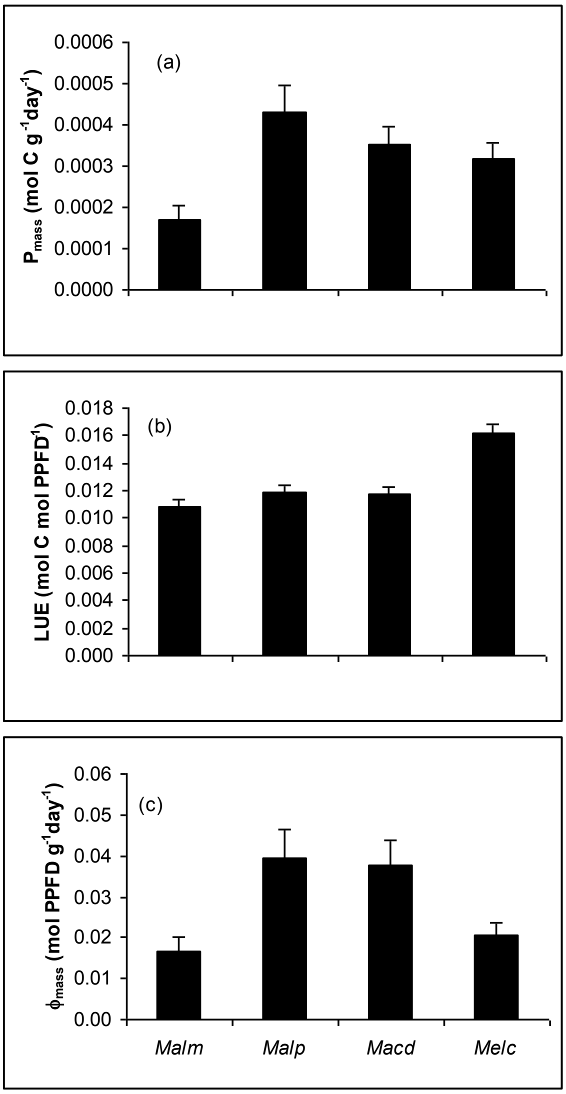

Fig. 5a-c P_{mass}, LUE and Φ_{mass} of pioneer species in stage IV. Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata; Melc, Melastoma candidum*. Bars denote standard error.

Table 4 Plant height, above ground mass, Specific Leaf Area (SLA), Leaf Mass Ratio (LMR), Leaf Area Ratio (LAR) and light capture per unit leaf area (ϕ_{area}) of pioneer species in stage IV

Species	n	height (m)	s.e.	plant mass (g)	s.e.	SLA (m^2g^{-1})	s.e.	LMR ($g\ g^{-1}$)	s.e.	LAR (m^2g^{-1})	s.e.	ϕ area (mol $m^{-2}day^{-1}$)	s.e.
Mallotus microcarpus	15	4.64^a	0.46	3427.29^a	781.74	0.0150^a	0.000	0.085^a	0.012	0.0013^a	0.000	12.77^a	2.03
Mallotus paniculatus	17	3.48^{abc}	0.27	570.72^b	145.23	0.0192^b	0.001	0.176^b	0.020	0.0033^b	0.000	12.96^a	1.89
Macaranga denticulata	19	4.08^{ab}	0.24	2024.41^{ac}	316.20	0.0151^a	0.001	0.150^b	0.009	0.0024^b	0.000	16.13^a	2.33
Melastoma candidum	19	2.95^c	0.16	1123.03^{abc}	254.23	0.0146^a	0.001	0.161^b	0.025	0.0025^{ab}	0.001	12.52^a	1.97

Notes: Values are means. Significance for species-effect (ANOVA) is indicated with different superscript letters (Bonferroni or Games-Howell post hoc test, p<0.05). Letter n indicates sample size and s.e. indicates standard error of the mean

Intraspecific differences in light capture and biomass allocation

The data of stages III and IV were used to compare differences in intraspecific competition as they differed in LAI, vegetation height and light extinction (Table 1). Stages I and II showed qualitatively the same data with respect to intraspecific competition as stage III, so for clarity we present only the data of stages III and IV.

In stage III Φ_{mass} did not increase with individual height (Fig. 6a & Table 5) (MM, p=0.130), indicating that there was no size-asymmetric competition for light within species. Values of Φ_{area} increased with individual height for *Mallotus microcarpus* and *Melastoma candidum* (Fig. 6b & Table 5) (MM, p=0.027) simply due to the fact that taller individuals reached the more illuminated layers of the canopy where they could capture more light. LMR and SLA decreased when individuals were taller (Table 5), thereby decreasing LAR (eq.(3)). The increase in Φ_{area} compensated for the loss in LAR, therefore Φ_{mass} remained constant with individual height within all species.

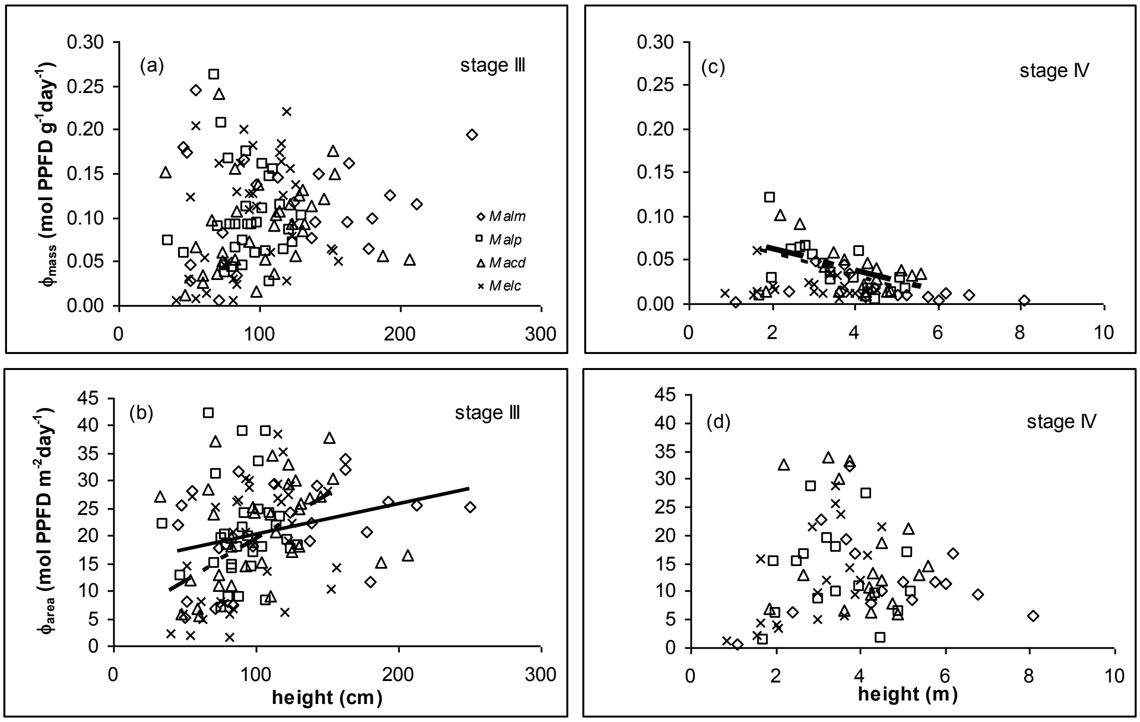

Fig. 6a-d Relation between Φ_{mass} and Φ_{area} and individual plant height in stage III (Fig. 6a-b) and IV (Fig. 6c-d). In (b) and (c) the regression lines indicate a significant relation ((b): solid line for *Malm*, broken line for *Melc* and (c) dashed line for *Malp*, broken line for *Macd*). Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata; Melc, Melastoma candidum*.

Table 5 Analysis of covariance (ANCOVA) with light capture per unit leaf area (ϕ_{area}), light capture per unit mass (ϕ_{mass}), Specific Leaf Area (SLA), Leaf Mass Ratio (LMR) and Leaf Area Ratio (LAR) as dependent variables and plant height as covariate

			Slope-effect		Height-effect		Species-effect	
Stage	Dependent	Covariate	F-value	p-value	F-value	p-value	F-value	p-value
III	ϕ_{area}	height	0.227	n.s.	4.871	0.027	0.746	n.s.
	ϕ_{mass}	height	1.014	n.s.	2.340	n.s.	3.015	0.035
	SLA	height	26.092	0.000	25.024	0.000	55.511	n.a.
	LMR	height	2.102	n.s.	4.892	0.029	3.565	0.017
	LAR	height	0.374	n.s.	0.314	n.s.	0.177	n.s.
IV	ϕ_{area}	height	2.701	n.s.	0.086	n.s.	0.639	n.s.
	ϕ_{mass}	height	1.932	n.s.	9.021	0.004	5.702	0.002
	SLA	height	1.622	n.s.	19.496	0.000	1.721	n.s.
	LMR	height	16.094	0.000	57.590	0.000	14.760	n.a.
	LAR	height	11.781	0.000	68.344	0.000	10.702	n.a.

Note: n.s. indicates a p-value greater than 0.05, n.a. means non-applicable

In stage IV, Φ_{mass} decreased with individual height for *Mallotus paniculatus* and *Macaranga denticulata* (Fig. 6c & Table 5). Φ_{area} was not correlated with individual plant height (Fig. 6d & Table 5). Apparently individuals had already reached the most illuminated layers of the canopy, so an increase in height did not increase Φ_{area}. The decrease in Φ_{mass} could be attributed to a decrease in LAR with individual height due to concomitant reductions in SLA and LMR (Table 5).

Discussion

Limited degree of size-asymmetric competition for light

When competition for a resource is asymmetric larger individuals get a disproportionately larger share of the available resource, which in turn can lead to increases in plant size inequalities. In our study, differences in light capture relative to size between species were present but relatively small and not related to plant size, thus the degree of asymmetric competition was very small. This result is in contrast to the general assumption that asymmetric competition for light is important as larger individuals shade shorter ones (see Weiner and Thomas 1986) but it is consistent with several studies on grasslands (Aan et al. 2006; Anten and Hirose 1999; Hirose and Werger 1995) and a secondary forest (Selaya et al. 2007) where similarity in light capture per unit mass between species of different size was also observed.

Asymmetric light competition was not observed between taller and smaller individuals within one species. This is in contradiction to Anten and Hirose (1998) who suggested that while light competition between species maybe size-symmetric, within species it is generally asymmetric. Other studies further reported that the degree of size-asymmetry in light competition increases with both the height and LAI of a vegetation stand (Aan et al. 2006; Anten and Hirose 1999; Hikosaka et al. 1999). We however did not observe such a trend: differences in light capture per unit mass (Φ_{mass}) between larger and smaller plants were not greater in the taller and denser stand (stage IV) than in the younger vegetation stages.

Growth per unit mass was independent of plant size both when comparisons were made among and within species. As a result, the relative height differences between species that were present at five months after field abandonment stayed more or less constant during the subsequent five years of succession. None of the species or individuals was outcompeted in the study period, nor did they seem to get outcompeted in the near future. Thus, the results in this study contradict the notion presented in the literature (Huston and Smith 1987; Van Breugel 2007) that in young secondary forest asymmetric competition for light should be the main mechanism shaping secondary forest dynamics. Our study does not preclude however that asymmetric competition may become more apparent in later stages of succession. Furthermore we did not consider below ground competition and as this often tends to be size-symmetric (Weiner 1986)-but see Hikosaka and Hirose (2001) where it was found to be asymmetric- it might have contributed to the size-symmetric growth observed by us.

The only other study that we know of that quantified light capture relative to plant size and related that to changes in size hierarchies in secondary tropical forest (the Bolivian Amazon, Selaya 2007), reported that during the first three years of succession taller species grew disproportionately fast compared to smaller ones (but species were measured simultaneously in different aged stands). This pattern was not so much related to larger species capturing disproportionately more light but rather to them having higher photosynthetic rates per unit of captured light (LUE). The discrepancy with our results might be related to differences in the overall growth rate of the plants at the two sites: at the Bolivian site the vegetation reached a height of 1.8 m on average within the first 6 months after field abandonment and 7.8 m after 3 years (Selaya 2007), a pattern also observed in another neotropical site (Mexico, Van Breugel 2007), while in our study in Vietnam it only reached 0.6 m in 5 months and 4.7 m after 5 years. Our study site was very degraded and probably had poor soil conditions. For the past 25 years it has been repeatedly used as a plantation site for *Acacia* trees (1 cycle takes 5-6 years). By contrast, the sites studied by Selaya (2007) and Van Breugel (2007) were in their first slash and burn agricultural cycle. Thus, as was predicted by Schwinning (1996), the degree of asymmetry in competition might be related to the overall rate of height increment and canopy development in a vegetation stand and not so much to the height or LAI ultimately achieved.

We could well explain the observed results of the limited occurrence of asymmetric growth and light competition in a mechanistic way using a canopy photosynthesis model, where photosynthetic rate per unit mass was used as a proxy for size dependent growth. The relative growth rate that was observed in the field was strongly correlated with the calculated photosynthetic rates per unit mass for species (r^2=0.87). Photosynthetic rate per unit of mass in turn was analysed as the product of light capture per unit mass, which is mainly determined by morphological plant traits, and light use efficiency, which is largely associated with physiological characteristics of plants (Anten and Hirose 2003). In general, taller plants captured slightly more light per unit leaf area (but not in vegetation stage IV), but due to species differences in LAR, light capture per unit mass, i.e. light capturing efficiency, was relatively similar for taller and smaller species and within species for taller and smaller individuals. Overall *Melastoma candidum* had the highest light use efficiency but other species were similar to each other. Regarding the leaf physiological traits that determine LUE, species mainly differed with respect to dark respiration and the associated light compensation point. Due to the relatively small differences in LUE and light capture per unit mass, differences in photosynthetic rates per unit mass between species were small too. This was reflected in the stable size hierarchy of the saplings in the field.

Pioneer species differed strongly in functional traits

Usually pioneers are grouped together as one functional group and compared with other functional groups with respect to light requirements (Chazdon 1992; King 1990; King 1994; Kitajima 1994; Poorter 2001; Poorter and Werger 1999; Selaya et al. 2007; Valladares et al. 2000). Implicitly they are therefore assumed to have similar functional traits. This study shows that pioneer species can have quite similar light capturing efficiencies and photosynthetic rates per unit mass but that they can differ considerably from each other when it comes to morphology and physiology, even when congeneric species are compared. The differences between the two *Mallotus* species were considerable. *Mallotus paniculatus* initially had an almost two-fold lower SLA than *Mallotus microcarpus* but its SLA increased in time while that of the other species remained constant. *Mallotus microcarpus* and *Mallotus paniculatus* also exhibited respectively the highest and the lowest values for light compensation point, dark respiration and P_{max}. The dark respiration and associated light compensation point differed at least four-fold between them.

Melastoma candidum showed the highest RGR and it could also very well keep up with vegetation height in the sapling stage. Since it is a shrub its inherent architecture inhibits it to grow tall (>5 m), but it was able to persist at least in the first five years of succession. *Melastoma candidum* produced many branches that were all directed upwards and leaves were placed at the growing tips of these branches (also found by Davies and Semui 2006) in the most illuminated layer of the crown, thereby increasing light capture per unit leaf area. More than 70% of the leaves were placed horizontally which is also favorable for light capture (Falster and Westoby 2003; Hikosaka and Hirose 1997; Muraoka et al. 1998). *Macaranga denticulata*, on the contrary hardly produced branches in vegetation stages I-III and also in stage IV branch mass was low compared to the other species (results not shown). However, it did make long petioles, thereby placing the leaves in lighter environments in order to increase light capture per unit leaf area (although this petiole trait is not incorporated in our model). The same phenomenon was observed for its congener *Macaranga gigantea* (Yamada et al. 2000).

Labeling for leaf turn over

Chapter 3

Whole canopy nitrogen-use efficiency of pioneer species in early secondary forest succession

with N.P.R. Anten

submitted

Abstract

The size hierarchy among plants during forest succession can be influenced by differences in nitrogen-use efficiency. During succession soil nitrogen availability decreases which increases the importance for species to use nitrogen efficiently. We compare whole canopy photosynthetic nitrogen-use efficiency ($PNUE_{cum}$) and its underlying traits among pioneer species in a tropical forest over the first years of succession. $PNUE_{cum}$ was largely determined by leaf life span and resorption and differed twofold among species. It was however not related to growth rates and only partly to species height. $PNUE_{cum}$ was slightly different within a species between successional stands that differed in height, leaf area index and resource availability, but an increase in competitive pressure did not result in major changes in the use of nitrogen. At the leaf level, potential PNUE (PPNUE: photosynthetic rate/leaf N content) was partly related to species growth rate but not to species height. Results showed that species that are generally considered part of the same functional group (pioneers) can differ considerably in nitrogen-use efficiency and its underlying traits.

Introduction

Differences in nutrient-use efficiency between species can partly determine their dominance and associated size hierarchies in plant communities (Aerts and Van der Peijl 1993). Nitrogen is an essential component of photosynthetic proteins (Evans 1989) and as a result of its limited availability it is one of the primary factors that limits plant growth in many natural ecosystems (Kachi and Hirose 1983; Vermeer and Berendse 1983). Even under non-limiting conditions its acquisition requires a large amount of energy (Field 1988). It is therefore important for plants to use nitrogen efficiently. Berendse and Aerts (1987) defined nitrogen-use efficiency (NUE) as the amount of dry matter that can be produced per unit of nitrogen. It can be calculated as the product of two components: nitrogen productivity (NP; rate of dry matter production per unit of nitrogen per unit of time) and the mean residence time (MRT) of nitrogen in a plant (the inverse of nitrogen turnover when plant growth is at steady state). At the leaf level nitrogen-use efficiency is often quantified as the ratio between photosynthetic capacity and leaf nitrogen content (potential photosynthetic nitrogen-use efficiency: PPNUE).

A high nitrogen productivity is associated with a high relative growth rate (Mediavilla and Escudero 2003; Reich et al. 1999; Reich et al. 1997). Leaves of fast growing species generally are low-cost leaves with high SLA (Garnier 1992; Poorter et al. 2005; Walters and Reich 1999), a short leaf life span (Coley 1988; Reich et al. 1992) and high investments of nitrogen in the photosynthetic machinery. These traits also facilitate high PPNUE (Poorter and Evans 1998; Poorter and Bongers 2006). Leaves of slow growing species show the opposite: low specific leaf area (SLA) with longer leaf life span and high nitrogen investment in cell walls (Onoda et al. 2004) as defense mechanisms against herbivory and physical damage (Coley 1988). They tend to have a lower nitrogen productivity and PPNUE but a longer mean residence time of nitrogen (Escudero et al. 1992; Wright et al. 2002). As a consequence of different growth characteristics for fast and slow growing species, there appears to be a trade-off between NP and MRT among species (Aerts 1989; Berendse and Aerts 1987; Silla and Escudero 2004).

The results above apply to comparisons between species native to different soil types. Comparisons between species growing on the same soil in a vegetation stand are much less common. In dense stands, light intensity declines from the top towards the bottom of the canopy (Monsi and Saeki 1953) and NUE would therefore be expected to depend on plant height and leaf area distribution. But plants occupying different positions in the canopy may have very different leaf nitrogen contents and photosynthetic characteristics (Anten and Hirose 2003; Han et al. 2004; Hikosaka and Hirose 2001; Yuan et al. 2004). Overall it has been found that differences in nitrogen-use efficiency tend to be small among such species growing in a single habitat in a stable vegetation stand (Hikosaka and Hirose 2000; Hikosaka et al. 2002; Yasumura et al. 2002). Hirose and Werger (1994) suggested that this similar resource use efficiency facilitates species co-existence in a stand.

In a regenerating forest, height and leaf area index of the vegetation rapidly increase (Swaine and Hall 1983; Uhl 1987) while light availability inside the canopy and soil nutrient availability (Ewel et al. 1991) decrease, causing species to increasingly compete. Thus an efficient use of nitrogen for biomass gain may partly determine a plant's success in such a competitive setting (Ellsworth and Reich 1996; Herbert et al. 2004; van der Werf et al. 1993). Studies have shown that in regenerating tropical rainforest early successional species tend to have higher leaf-level PPNUE and faster growth than species that appeared later in succession (Reich et al. 1994; Selaya 2007). The question however remains how whole canopy NUE compares among pioneer species. During the first phase of succession there is generally intense competition between pioneers and even small differences in nitrogen-use efficiency may partly explain the size hierarchy among species.

As noted nitrogen-use efficiency is a function of a suit of traits including leaf life span, nitrogen resorption, leaf-level PPNUE but also plant height, crown structure, leaf area and nitrogen distribution. However, very little work that we know of has been done to quantitatively link these traits to nitrogen-use efficiency. Hiremath (2000) developed a concept to study the different components that determine leaf life time nitrogen-use efficiency in a detailed and integrated manner (see also Funk and Vitousek 2007). She defined cumulative photosynthetic nitrogen-use efficiency as the ratio of total carbon assimilation by a leaf (integrated over the life span of a leaf taking a decline in photosynthetic rates with leaf age into account) to total nitrogen investment in that leaf over its lifetime. Since her experiment was performed at leaf-level in an experimental plantation, traits such as plant height (i.e. canopy position), whole canopy light capture and nitrogen distribution in the canopy were not taken into account.

Here we report a study in which nitrogen-use efficiency at the canopy level is compared among early successional species over the first years of succession. Whole canopy cumulative photosynthetic nitrogen-use efficiency (with adaptations as compared to Hiremath 2000) is compared between four pioneer species at two stages of succession (1.5 and 5 year old forest) in a strongly degraded secondary forest in Vietnam (see chapter 2). We relate nitrogen-use efficiency to the size hierarchy among species. Based on previous findings (Reich et al. 1994; Selaya 2007) we predict that taller plants have a higher whole canopy nitrogen-use efficiency than smaller plants.

Methods

Study area

The study site is located in the buffer zone of Bach Ma National Park, Thua Thien Hue Province, in central Vietnam (16°10'N 107°50'E). Bach Ma National Park and its buffer zone were established in 1991 with a total area of 43,331 ha. It is the core of the last remaining contiguous forest belt in Vietnam, stretching from the South China Sea to the border with Laos. The area experiences high rainfall, especially from November until February (up to 8,000 mm per year). There is no distinct dry season and the vegetation is evergreen (Tran and Ziegler 2001). The study site was used for monoculture plantations of *Acacia mangium* after defoliation and destruction in the second Indochina war. Part of the site was left fallow in 1999. Secondary forest succession started and by 2004 a 5 year old forest stand (hereafter 5 y/o stand) had developed.

Species selection

We selected four study species in 2004, all co-dominant in the stand: the shrub, *Melastoma candidum* (Melastomataceae) and three tree species, *Mallotus microcarpus*, *Mallotus paniculatus* and *Macaranga denticulata* (all Euphorbiaceae). They represented over 75% of the total plant cover and were the only woody species present in sufficient numbers for study. Plants therefore predominantly interacted with conspecifics or with plants of the three other selected species. Species of *Melastoma* (Davies and Semui 2006), *Mallotus* and *Macaranga* (Lee et al. 2005; Slik et al. 2003; Toma et al. 2005) are known to regenerate on deforested or degraded lands and are characteristic of secondary forests in South-East Asia (Primack and Lee 1991; Steenis 1965). We selected plants for inclusion in this study from a 2 ha area making sure they covered the entire height range (up to 8 m high). The surrounding vegetation consisted of ferns (*Dicranopteris linearis*), grasses (*Phragmites communis, Imperata cylindrica*) and lianas. Later successional species were absent at this stage.

Measurements

Measurements on the individuals in the 5 y/o stand were done in September and October of 2004. Light climate, LAI, biomass allocation and nitrogen content of leaves were determined per individual (see chapter 2) so that photosynthetic rates could be calculated (see section '*Calculation of whole canopy photosynthesis*'). In November 2004 the area was experimentally slashed and burned. After ~0.5 years 50 individuals per species divided over 10 plots of 25m^2 each, were randomly selected. After approximately 1.5 years (hereafter 1.5 y/o stand) we measured light climate, LAI, biomass allocation and the nitrogen content of young fully exposed leaves (2-3) in top of the canopy of each individual (see chapter 2) in order to calculate photosynthetic rate (see section '*Calculation of whole canopy photosynthesis*'). Growth data of the saplings and data on photosynthetic traits of each species were taken from chapter 2.

The 1.5 y/o and the 5 y/o stand differed in height and Leaf Area Index (LAI). The mean vegetation height in the 1.5 y/o stand was 1.4 m (±0.41 m) and the LAI was 3.73 (±0.75). In the 5 y/o stand vegetation height was 4.71 m (±1.54 m) and the LAI was 5.72 (±1.16) (see Table 1 and Fig. 1c & d in chapter 2).

Leaf life span was measured on 7 individuals per species growing in the study plots for a period of one year. Every month the newest leaves were marked with a straw. Newly developed leaves and old leaves (including the ones with a straw) were counted monthly to obtain leaf production and leaf loss rates. Since the plants were still growing they were not at steady state, thus leaf life span was calculated as the number of leaves on the plant, divided by the average of the slopes of cumulative leaf production and leaf loss (King 1994). We did not measure leaf life span in the 5 y/o stand.

Nitrogen resorption was determined by measuring leaf nitrogen content of yellow leaves (4-6) of each species. The nitrogen resorped was expressed as a fraction of the average nitrogen content of young fully exposed leaves in the top of the canopy.

Calculation of whole canopy photosynthesis

The model used here is almost identical to the one used by Anten and Hirose (2003) and was described into detail by them. In chapter 2 a short description is given including references to equations used by them.

The light response of net leaf photosynthesis (P in µmol $m^{-2}s^{-1}$) was characterised by a non-rectangular hyperbola (Johnson and Thornley 1984):

$$P = (((P_{max}+\Phi I_L)-[(P_{max}+\Phi I_L)^2 - 4\theta Pmax\Phi_L]^{0.5})/2\theta)-R_d \qquad (1)$$

where P_{max} is the maximum photosynthetic rate, I_L the absorbed photon flux, R_d the dark respiration, Φ the quantum yield (calculated from measured values) and θ the curvature factor (set to 0.8, see Hirose et al. 1997).

P_{max} was calculated as a function of leaf nitrogen content per unit leaf area (N_{area}) (Anten et al. 1995):

$$P_{max}=a*N_{area}+b \qquad (2)$$

with a the slope and b the intercept of the relation.

Calculation of the distribution of light saturated photosynthetic rates in the sapling's crown was done as a function of the nitrogen (N) distribution (Hirose and Werger 1987). For the 5 y/o stand we used the measured nitrogen distribution. In the 1.5 y/o stand nitrogen content was only measured in the most illuminated leaves in the top of the canopy (N_o). We calculated the nitrogen distribution in the canopy (N_{area}: mmol m^{-2}) using the equation proposed by Anten (1997): $N_{area}=N_o(I/I_o)^{0.4}$ with I/I_o the relative light intensity. This equation shows that the nitrogen distribution scales with the light distribution by a power 0.4. This is based on the mean distribution of nitrogen in various stands reviewed by Anten (1997) and it is also similar to the nitrogen distribution found in this study in the 5 y/o stand (scaling coefficient 0.32-0.45).

Calculation of nitrogen-use efficiency

Potential photosynthetic nitrogen-use efficiency (PPNUE: µmol C mmol $N^{-1}s^{-1}$) was calculated as:

$$PPNUE=P_{max}/N_o \qquad (3)$$

with P_{max} as the maximum photosynthetic rate (µmol C $m^{-2}s^{-1}$) of young fully exposed leaves and N_o as the nitrogen content per unit area of young fully exposed leaves (mmol N m^{-2}).

Whole canopy cumulative PNUE ($PNUE_{cum}$: mol C mmol N^{-1}) was calculated as:

$$PNUE_{cum} = (P_{daily} * LLS) / ((N_{total}) * (1-r)) \quad (4)$$

where the numerator is the whole canopy daily carbon gain (P_{daily}: mol C g $leafmass^{-1}day^{-1}$) multiplied by the leaf life span (LLS: days). The denominator is the amount of nitrogen invested in a gram of leaf over its life span and then lost from the plant, i.e. the product of whole canopy foliar nitrogen content (N_{total}: mmol g^{-1}) and the fraction of nutrients not resorped before leaf abscission ((1-r), in which r indicates resorption). This formula is based on the calculation for cumulative PNUE in Hiremath (2000) with the main exception that carbon gain and nitrogen content are determined for the whole canopy, thus including leaves of different age.

Equation (4) can be divided into two parts, i.e. whole canopy Photosynthetic Nitrogen Productivity (PNP: mol C mmol $N^{-1}day^{-1}$) and mean residence time (MRT, days) of nitrogen.

$$PNP = P_{daily}/N_{total} \quad (5)$$

and

$$MRT = LLS/(1-r) \quad (6)$$

MRT was compared between species but we did not consider intraspecific variation in this trait (Hiremath et al. 2002).

Statistics

Even though plots were established only to be able to trace back the saplings in the following measuring period, both plot-effects and also individuals-effects have occurred. Therefore analyses regarding the 1.5 y/o stand were done with Linear Mixed Effects Model (in results section abbreviated as MM). Normality and Levene's tests were done. Whenever necessary, data were (log)transformed. When values of variables were analysed between species, plot number was identified as subject. The effect of species on the average values of N_o, P_{max}, PPNUE, height, plant mass, RGR, SLA, PNP and $PNUE_{cum}$ was determined by identifying these variables as dependent and species as factor. When designing the model, species was the sole fixed effect, including intercept. For random effect an intercept was included for the subject plot number, but no model for random effects was designed. No post-hoc tests were available but most between-species differences could be deduced from the parameter estimates. When the change in PNP between species was analysed with height, subjects included plot number and individual number. The variable on the y-axis was the dependent (PNP), the variable on the x-axis the covariate (height) and species was the factor. Slope-effects were tested by designing a model with an interaction term of the fixed effects ‘species’ and ‘height’. If a significant slope-effect was absent (P>0.05), the test was repeated with both fixed effects as main effects. For random effect an intercept was included for the subjects ‘plot number’ and ‘individual number’, but no model for random effects was designed.

For the 5 y/o stand the effect of species on the average values of N_o, P_{max}, PPNUE, height, plant mass, SLA, PNP and $PNUE_{cum}$ were analyzed using ANOVA tests. Post-hoc tests, either Bonferroni (equal variances assumed) or Games-Howell (equal variances not assumed), were done to test for differences among species. To test for species differences in the relation between PNP and individual height, an ANCOVA test was used. If a significant slope-effect was absent (P>0.05), ANCOVA was repeated with the species and the height only as main effects.

The differences in slopes of the P_{max}-N_{area} relation was analysed with an ANCOVA test and the differences in leaf life span and mean residence time were tested with an ANOVA test with a Bonferroni post hoc test.

Results

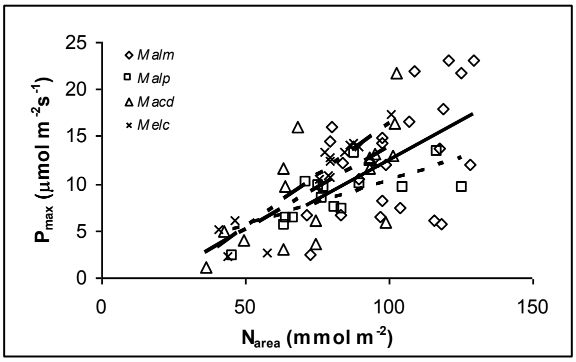

Fig. 1 Relation between maximum photosynthetic rate (P_{max}) and nitrogen content of leaves (N_{area}) of pioneer species. Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata; Melc, Melastoma candidum*. Regression lines are depicted: solid line for *Mallotus microcarpus*, dashed line for *Mallotus paniculatus*, fine broken line for *Macaranga denticulata* and coarse broken line for *Melastoma candidum*.

From the photosynthesis measurements the species-specific relation between maximum photosynthetic rates (P_{max}) and nitrogen content in the leaf (N_{area}) was determined (Fig. 1). All species showed an increase in P_{max} with an increase in N_{area}. Slopes were not significantly different among species (ANCOVA, p=0.404). The formulas describing these relations and the maximum nitrogen content of young fully exposed leaves (N_o) of the trees in the plots were used to calculate maximum photosynthetic capacity per unit leaf area (P_{max}) of the trees in the plots (Table 1). Dividing P_{max} by N_o gave potential photosynthetic nitrogen-use efficiency (PPNUE) (eq.(3)). Differences between species and between stands were small but in both stands *Melastoma candidum* showed the highest, *Mallotus microcarpus* and *Macaranga denticulata* intermediate, and *Mallotus paniculatus* the lowest PPNUE.

Table 1 Mean values of maximum leaf nitrogen content (N_o) of leaves in the top of the canopy, maximum photosynthetic rate (P_{max}) of leaves in the top of the canopy and potential photosynthetic nitrogen-use efficiency (PPNUE) of trees in the field

Species	n	N_o (mmol m^{-2})	s.e.	p-value	P_{max} (µmol $m^{-2}s^{-1}$)	s.e.	p-value	PPNUE (µmol C mmol $N^{-1}s^{-1}$)	s.e.	p-value
1.5 y/o stand				0.023			0.014			0.000
Mallotus microcarpus	38	89.81	4.81		10.83	0.81		0.121	0.003	
Mallotus paniculatus	38	74.26	3.73		7.81	0.36		0.105	0.000	
Macaranga denticulata	38	83.30	2.60		10.91	0.46		0.131	0.002	
Melastoma candidum	37	77.45	4.25		11.30	0.94		0.146	0.004	
5 y/o stand										
Mallotus microcarpus	15	109.28	6.83	a	14.10	1.15	ac	0.129	0.003	a
Mallotus paniculatus	17	93.21	8.38	a	9.63	0.80	b	0.103	0.001	b
Macaranga denticulata	19	92.63	3.21	a	12.57	0.57	bc	0.136	0.002	a
Melastoma candidum	19	100.61	5.78	a	16.43	1.28	a	0.163	0.003	c

Notes: Values are means. Significance levels (p-values) of the overall species-effects are shown and letters indicate significance of the ANOVA post-hoc tests ($p<0.05$). Letter n indicates sample size and s.e. indicates standard error of the mean

Growth data (Relative Growth Rate: RGR) were taken from chapter 2. Plant mass was measured non-destructively several times after the slash and burn treatment on the same individuals. *Melastoma candidum* showed the highest relative increase in mass (MM, $p<0.001$) (RGR: Table 2) in the period from 150-510 days after the slash and burn treatment which corresponded to its high PPNUE. The other species did not show significant differences in RGR. Mean species height (Table 2) and PPNUE were not related in both stands. In the 1.5 y/o stand the smallest species, *Mallotus paniculatus*, had the lowest PPNUE but for the other species and in the 5 y/o stand no relation was found. The tallest species, *Mallotus microcarpus*, had intermediate values of PPNUE in both stands. The species with the highest PPNUE, *Melastoma candidum*, had the longest leaf life span while the species with lowest PPNUE, *Mallotus paniculatus*, had an intermediate leaf life span (Tables 1 and 2). They both had intermediate values of SLA in the 1.5 y/o stand. In the 5 y/o stand SLA was highest for the species with the lowest PPNUE, *Mallotus paniculatus*, and lowest for the species with the highest PPNUE, *Melastoma candidum*.

Table 2 Mean values of height, above ground mass, relative growth rate (RGR), leaf life span (LLS) and specific leaf area (SLA) of pioneer species

Species	n	height (m)	s.e.	p-value	mass (g)	s.e.	p-value	RGR (mg $g^{-1}day^{-1}$)	s.e.	p-value	LLS (day)	s.e.	p-value	SLA ($m^2 g^{-1}$)	s.e.	p-value
1.5 y/o stand				0.00			0.00			0.00						0.000
Mallotus microcarpus	22	1.21	0.13		48.2	14.6		6.52	0.57		88	4	a	0.0163	0.000	
Mallotus paniculatus	32	0.91	0.04		11.5	1.4		7.42	0.33		106	4	b	0.0134	0.000	
Macaranga denticulata	34	1.05	0.07		25.5	3.6		8.02	0.27		108	4	b	0.0155	0.000	
Melastoma candidum	35	0.95	0.05		29.9	9.9		9.63	0.43		143	10	c	0.0133	0.000	
5 y/o stand																
Mallotus microcarpus	15	4.64	0.46	a	3427.3	781.7	a	-	-	-	-	-	-	0.0151	0.000	a
Mallotus paniculatus	17	3.48	0.27	abc	570.7	145.2	b	-	-	-	-	-	-	0.0192	0.001	b
Macaranga denticulata	19	4.08	0.24	ab	2024.4	316.2	ac	-	-	-	-	-	-	0.0151	0.001	a
Melastoma candidum	19	2.95	0.16	c	1123.0	254.2	abc	-	-	-	-	-	-	0.0146	0.001	a

Notes: Values are means. Significance levels (p-values) of the overall species-effects are shown and letters indicate significance of the ANOVA post-hoc tests ($p<0.05$). Letter n indicates sample size and s.e. indicates standard error of the mean

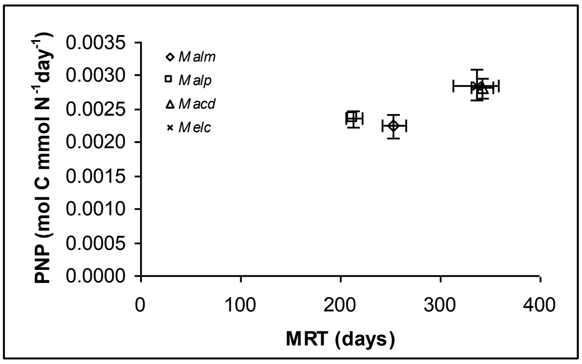

Fig. 2 Whole canopy photosynthetic nitrogen productivity (PNP) and mean residence time (MRT) of nitrogen of four pioneer species in a 1.5 y/o forest stand. Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata; Melc, Melastoma candidum*. Bars denote standard error.

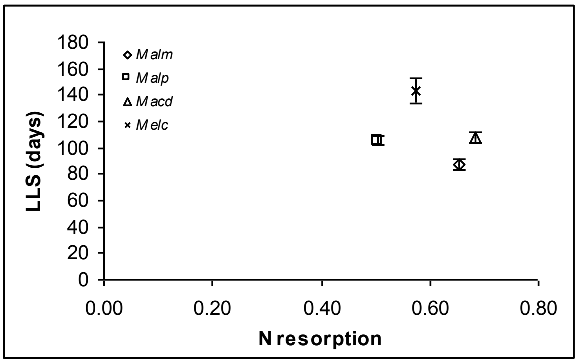

Fig. 3 Leaf life span (LLS) and resorption of nitrogen of four pioneer species in a 1.5 y/o forest stand. Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata; Melc, Melastoma candidum*. Bars denote standard error.

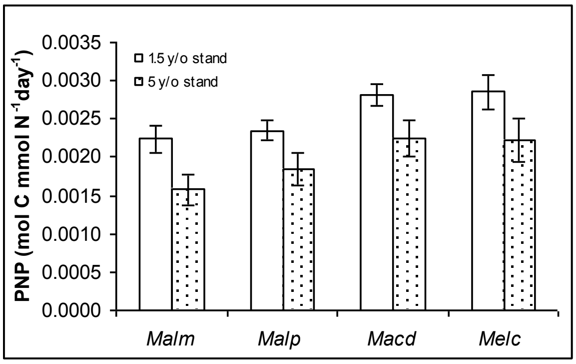

Fig. 4 Whole canopy photosynthetic nitrogen productivity (PNP) of four pioneer species in two successional forest stands. Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata; Melc, Melastoma candidum*. Bars denote standard error.

We determined photosynthetic nitrogen productivity (PNP) (eq.(5)) and mean residence time (MRT) (eq.(6)) of nitrogen for the saplings in the 1.5 y/o stand (Fig. 2). There were no differences in PNP between species (MM, p=0.051) despite differences in species height and RGR. Species differed in MRT with *Macaranga denticulata* and *Melastoma candidum* showing significantly higher values than *Mallotus microcarpus* and *Mallotus paniculatus* (ANOVA, p<0.001). There tended to be a positive relation between PNP and MRT. The latter consists of two omponents: leaf life span (LLS) and resorption (eq.(6)) (Fig. 3). LLS was highest for *Melastoma candidum* and lowest for *Mallotus microcarpus* (ANOVA, p<0.001). *Mallotus paniculatus* and *Macaranga denticulata* had intermediate values. Resorption values ranged from 51% for *Mallotus paniculatus* to 69% for *Macaranga denticulata*.

PNP was lower in the 5 y/o stand than in the 1.5 y/o stand for all species (Fig. 4) (ANOVA, p=0.021, 0.029, 0.042 for *Mallotus microcarpus*, *Mallotus paniculatus* and *Macaranga denticulata* resp.), except for *Melastoma candidum* (ANOVA, p=0.101). In the 5 y/o stand there were no differences between species for PNP (ANOVA, p=0.207).

Fig. 5 shows whole canopy cumulative PNUE (PNUE$_{cum}$). In both stands *Macaranga denticulata* and *Melastoma candidum* showed significantly higher values than *Mallotus microcarpus* and *Mallotus paniculatus* (ANOVA, p<0.001 and MM, p<0.001 for the 1.5 y/o and the 5 y/o stand respectively). PNUE$_{cum}$ in the 5 y/o stand was lower than in the 1.5 y/o stand for *Mallotus microcarpus*,

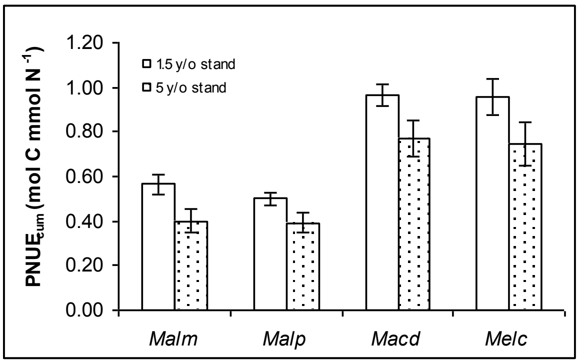

Fig. 5 Whole canopy cumulative photosynthetic nitrogen-use efficiency (PNUE$_{cum}$) of four pioneer species in two successional forest stands. Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata; Melc, Melastoma candidum*. Bars denote standard error.

Mallotus paniculatus and *Macaranga denticulata* (ANOVA, p=0.021, 0.029 and 0.042 respectively) but not for *Melastoma candidum* (ANOVA, p=0.101). There was no distinct relation between RGR and PNUE$_{cum}$. In general, PNUE$_{cum}$ was high for *Melastoma candidum*, the smallest species with the longest leaf life span, and low for *Mallotus microcarpus*, the tallest species with shortest leaf life span.

We did not consider intraspecific variation in MRT, therefore only PNP is plotted against individual height to test for within species variation (Fig. 6). Only for *Melastoma candidum* a significant positive relation was observed between PNP and individual height in both stands (linear regression, p=0.011 and 0.008 for the 1.5 y/o and the 5 y/o stand respectively).

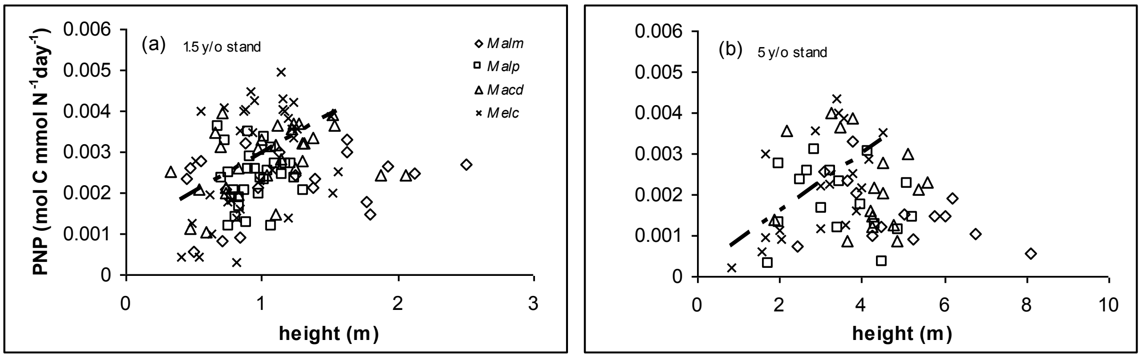

Fig. 6a-b Relation between photosynthetic nitrogen productivity (PNP) and individual plant height of four pioneer species in a 1.5 y/o (a) and a 5 y/o (b) secondary forest stand. Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata; Melc, Melastoma candidum*. Regression lines are depicted for *Melastoma candidum* in both windows.

Discussion

Cumulative photosynthetic nitrogen-use efficiency (PNUE$_{cum}$) differed twofold among species but was not related to species growth rate and only partly related to species height. Nitrogen-use efficiencies of species were quite similar between successional stands, indicating that a higher leaf area index and lower resource availability leading to higher competitive pressure did not result in major changes in the use of nitrogen.

Cumulative photosynthetic nitrogen-use efficiency (PNUE$_{cum}$) is the product of two components: photosynthetic nitrogen productivity (PNP) and mean residence time (MRT). PNP did not differ between species despite differences in species height. Yasumura et al. (2002) found that canopy species in a beech forest had higher nitrogen productivity than understory species, but the height difference between the species in their study was much greater than in ours (16 m for canopy species, 1-2 m for understory species). Furthermore differences in light levels were much greater than in our study where differences in species height and light levels were relatively small (see similar average values of Φ_{area} among species in Table 3 & 4 in chapter 2). In the 5 y/o stand PNP was lower for most species than in the 1.5 y/o stand. This can be attributed to lower light levels in general in the 5 y/o stand as the LAI was greater and leaves were therefore on average more shaded.

PNP can also be determined by differences in leaf-level PPNUE. The pioneer species in this study showed small differences in potential photosynthetic nitrogen-use efficiency (PPNUE), which partly contributed to species having a similar PNP. Plants with a high potential growth rate are thought to have high nitrogen investments in the photosynthetic machinery, causing them to have high PPNUE (Poorter and Evans 1998; Poorter and Bongers 2006). In this study growth rate was only partially correlated to PPNUE: the species with the highest RGR had the highest PPNUE, but for the other species no such relation was found. Reich et al. (1994) did find a relation between growth rate and PPNUE and also Selaya (2007) found that a high PPNUE was related to dominance of species early in succession. They however studied early versus later successional species. In our study, all species are early pioneers. Within a community growth characteristics and associated growth rates are believed to be more similar among pioneers than between pioneers and later successionals (Poorter 2006). Since only four species were studied here this could explain why, contrary to other studies, we did not find a relation between PPNUE and other leaf traits such as SLA and leaf life span.

Species height growth rate (which can be directly correlated to species height in this case) was not correlated with PPNUE either, in contrast to what was found by Poorter and Bongers (2006). In the 1.5 y/o stand species height differences were still small. In the 5 y/o stand they were more pronounced and the competitive pressure for resources was higher but also in this stand height was not correlated to PPNUE.

In our study no trade-off between the two components of $PNUE_{cum}$ (PNP and MRT) was found. In general species that tended to have a higher PNP also had a higher MRT. When different species with short leaf life span (<1 year) were compared, this trade-off has been found to be very weak or absent (Aerts and de Caluwe 1994; Vazquez de Aldana and Berendse 1997; but see Yasumura et al. 2002). Thus the degree to which there is a trade-off between nitrogen productivity and MRT largely depends on the degree of interspecific variation in leaf life span. When this is relatively small there is no such trade-off and variation in other traits influencing nitrogen-use efficiency become more important (Eckstein et al. 1999; Escudero et al. 1992). In our study resorption and leaf life span both influenced MRT. The amount of days that a unit of nitrogen circulated in the plant's canopy was twice as long as leaf life span for *Mallotus paniculatus* while it was more than three times as long for *Macaranga denticulata*. This difference is caused by their different resorption efficiencies (51% for *Mallotus paniculatus*; 69% for *Macaranga denticulata*). Thus resorption is of great influence on MRT.

Species with higher MRT had approximately twofold higher $PNUE_{cum}$ than species with lower MRT. Differences in $PNUE_{cum}$ were not related to species growth rates and only partly to species height with the tallest species having a low $PNUE_{cum}$ and the smallest species a high $PNUE_{cum}$. This is opposite to what we predicted. It might be due to the fact that in our study $PNUE_{cum}$ appeared to be largely determined by MRT and not by the plant's position in the canopy and its concomitant NP. Hiremath (2000) found that the species with the longest leaf life span, a later successional tree species, had a higher cumulative photosynthetic nitrogen-use efficiency than a early successional tree species. Similar results were obtained here: the species with the longest leaf life span had a two-fold higher $PNUE_{cum}$ than the species with the lowest leaf life span.

Hiremath (2000) found a two-fold difference in cumulative photosynthetic nitrogen-use efficiency between early and later successional species. We found the same degree of difference among only pioneer species. Usually pioneers are grouped together as one functional group (King 1994; Selaya et al. 2007). Implicitly they are therefore assumed to have similar functional traits. However, this study shows that leaf functional traits can differ considerably between pioneer species (see also chapter 2 and Dalling et al. 2004) and that this can result in substantial differences in nitrogen-use efficiency. In contrast to what was previously found by others (Hikosaka and Hirose 2000; Hikosaka et al. 2002; Hirose and Werger 1994) these results show that species growing in the same habitat can show differences in nitrogen-use efficiency, even though species composition was stable during several years in this system (see chapter 2).

In this study nitrogen-use efficiency was not calculated based on N contents of litter as is done by others (Herbert and Fownes 1999; Smith et al. 1998; Yasumura et al. 2002). When we did, it appeared that the results were in the same order of magnitude, albeit slightly lower (calculations not shown). It has to be pointed out that calculations based on litter assume steady-state conditions with respect to leaf production and leaf loss. In our study plants were growing and therefore not in steady-state. This could have lead to underestimations when the nitrogen-use efficiency was calculated based on litter.

A high MRT is likely to be advantageous in nutrient limited environments, where nutrient conservation rather than rapid growth is the key to persistence (Hiremath 2000). Slash and burn practices lead to land degradation (Gehring et al. 2005; Styger et al. 2007). Even though fires increase nutrient availability for a short time (Kennard and Gholz 2001; Soto et al. 1995), biomass growth during secondary succession is inhibited due to nutrient limitation (Davidson et al. 2004). The number of slash and burn cycles and the fallow length influence the availability of soil nutrients (Bruun et al. 2006; Lawrence et al. 2005) and this affects species composition of the vegetation (Paniagua et al. 1999). It was previously found that on soils with low fertility, species with high MRT instead of high PNP are favored (Aerts and de Caluwe 1994; Vazquez de Aldana and Berendse 1997; Yuan et al. 2005). Our study site was very degraded due to effects of war followed by several slash and burn cycles of 5-6 years with very short fallow lengths (several months) thus a high nutrient retention and an efficient use of resources seems beneficial here (see also dos Santos et al. 2006).

So far we have discussed interspecific differences in nitrogen-use efficiency. For intraspecific differences we only considered PNP since resorption and leaf life span appeared to be similar for individuals within a species. For *Melastoma candidum* individuals PNP increased with an increase in height. However, no such relation was found for the other species. Others found taller individuals in monostands to experience higher light levels and as a result they had higher nitrogen productivity than smaller individuals (Han et al. 2004; Hikosaka and Hirose 2001; Yuan et al. 2004). Our vegetation stand was less homogeneous than the mentioned monostands. As a result individuals of different height experienced relatively similar light conditions (see Φ_{area} data in Fig. 6 in chapter 2). Since *Melastoma candidum* is a shrub, its inherent architecture inhibits it to grow tall, it could not reach the most illuminated layers of the canopy by growing tall like the other species. Instead, it produced many branches that were all directed skywards and leaves were placed at the growing tips of these branches (also found by Davies and Semui 2006) in the most illuminated part of its crown, thereby increasing light capture per unit leaf area (see chapter 2). More than 70% of the leaves were placed horizontally which is also favorable for light capture (Falster and Westoby 2003; Hikosaka and Hirose 1997; Monsi and Saeki 1953; Muraoka et al. 1998). Thus instead of growing tall, *Melastoma candidum* reaches illuminated environments by efficient leaf positioning.

Liberated pioneer tree (1.5 year old stand)

Chapter 4

Tree liberation to accelerate secondary forest succession: a model approach

with N.P.R. Anten, R.J. Oomen and F. Schieving
submitted

Abstract

Excessive growth of non-woody plants and shrubs on degraded lands can strongly hamper tree growth and thus secondary forest succession. One often used method to accelerate succession, called liberation, is opening up the vegetation canopy around young target trees. This can increase growth of target trees by reducing competition for light with neighboring plants. Due to the different light requirements of target species, liberation has not always had the desired effect. Here we present a 3D-model which calculates photosynthetic rate of individual trees in a vegetation stand. It enables us to examine how stature, crown structure and physiological traits of target trees and characteristics of the surrounding vegetation together determine the growth of trees. Various types of management practices can be simulated. The model was applied to a liberation experiment that we conducted on pioneer species in a young secondary forest in Vietnam. Species responded differently to the treatment depending on their height, crown structure and their shade-tolerance level. The responses were also dependent on the height and density of the vegetation and the gap radius from which it was removed. There were strong correlations between calculated photosynthetic rates and observed growth, indicating that the model was well able to predict growth of trees in young forests and the effects of a commonly applied practice there upon. With the approach presented here we can simulate vegetation removal in different scenarios. As such it provides a useful tool in planning liberation activities without performing costly and long-lasting experiments.

Introduction

In tropical regions the area of secondary forests is expanding due to the increased pressure on primary forests. However, natural forest regeneration after disturbance is often slow or stagnates, many times caused by excessive growth of shrubs, lianas or grasses (Aide et al. 1995; Chapman and Chapman 1999; Guariguata and Dupuy 1997; Hooper et al. 2004). Often these plants invade degraded sites and they may compete with trees for resources (Berkowitz et al. 1995; Holl 1998; Parrotta et al. 2002; Putz and Canham 1992) or catch fire in the dry season that destroys young forest growth (Werger 1983). This strongly hampers forest succession.

In recent years there has been increased attention for restoration ecology and in particular for management options to accelerate recovery of forests (Holl and Kapelle 1999; Parrotta et al. 1997). One often used method to increase tree growth and thus facilitate more rapid succession is opening up the vegetation surrounding target individuals (Chapman and Chapman 1999; Dolanc et al. 2003; Duncan and Chapman 2003; Fuhr et al. 2001). This method, called liberation, can stimulate growth of these individuals by reducing competition with neighboring plants, especially competition for light. However, liberation has not always had the desired effect (Chapman et al. 2002; Collet et al. 1998; De Graaf et al. 1999; Otsamo 2000).

Liberation increases light levels at which target trees grow. Studies have shown that tree species have different light requirements (Dupuy and Chazdon 2006; Montagnini et al. 1997; Ramos and del Amo 1992), even closely related ones (Ådjers et al. 1995), and this can change within a tree with tree age (Davidson et al. 2002). Thus the light levels created by liberation may be suitable for some species and some individuals but not for others. Forest managers need to know when, where and how to intervene to accelerate forest succession. However, experiments require a lot of time, space and money and the outcome is usually restricted to a specific set of species in a specific setting and a limited amount of experimental conditions (for instance gap size) that are created (see Paquette et al. 2006 and references therein).

In this study we therefore present a three-dimensional model (see '*Model description*') which enables us to examine how stature, crown structure and physiological traits of the target trees and the density and height of the surrounding vegetation in concert determine the growth of target trees. Height, crown dimensions, leaf area, leaf angle distribution and leaf physiological characteristics of target trees can be varied. The characteristics of the surrounding vegetation (Leaf Area Index, leaf angle distribution, height) can also explicitly be specified and the effects of various types of management practices (e.g. gap creation) can be simulated.

The model will be applied to a dataset from a young natural secondary degraded forest in Vietnam. Saplings of pioneer tree species that recruited after a slash and burn treatment were monitored over time (see chapter 2). In the 1.5 year old vegetation stand 50% of the individuals were liberated of surrounding vegetation. With model calculations we determine the effect of liberation of individual trees of three woody species in terms of light capture and photosynthesis and relate this to growth of the target trees. The validity of the model is critically tested by comparing predicted tree photosynthetic rates for a given point in time to subsequent growth rates. We also simulate the effects of vegetation LAI and height and gap radius in vegetation removal events, and we determine the effect of liberating target trees in stands of different successional status.

Methods

Study area

The study site is located in the buffer zone of Bach Ma National Park, Thua Thien Hue Province, in central Vietnam (16°10'N 107°50'E). Bach Ma National Park and its buffer zone were established in 1991 with a total area of 43,331 ha. It is the core of the last remaining contiguous forest belt in Vietnam, stretching from the South China Sea to the border with Laos. The area experiences high rainfall, especially from November until February (up to 8,000 mm per year). There is no distinct dry season and the vegetation is evergreen (Tran and Ziegler 2001). After defoliation in the war, the study site was used for monoculture plantations of *Acacia mangium*. Part of the site was left fallow in 1999.

Study species

In November 2004 we applied a slash and burn treatment (see chapter 2 for details). The woody species that recruited afterwards were monitored over time. For this study three tree species were selected: *Mallotus microcarpus*, *Mallotus paniculatus* and *Macaranga denticulata* (all Euphorbiaceae). Species of *Mallotus* and *Macaranga* are known to regenerate on deforested or degraded lands (Lee et al. 2005; Slik et al. 2003; Toma et al. 2005) and are characteristic of secondary forests in South-East Asia (Primack and Lee 1991; Steenis 1965). The role of these pioneer tree species in succession is important as they have the ability to overgrow grass and shrub species that may strongly hamper succession (see also Finegan 1984; 1996).

Measurements

Measurements were done in April 2006, 1.5 years after the slash and burn treatment (1.5 y/o stand hereafter). Crown allometry of the individual target trees (20 individuals for *Mallotus microcarpus*, 31 for both *Mallotus paniculatus* and *Macaranga denticulata*) was determined by measuring crown dimensions in four wind directions and from the bottom to the top of the crown. Biomass allocation, photosynthetic characteristics and nitrogen contents of the same individuals and data on the light climate in which they grew were measured at the same time (see chapter 2 for methods).

After finishing the measurements half of the individuals were selected randomly distributed over the study area to be removed of surrounding vegetation ('liberated plants'). All vegetation (shrubs, grasses, lianas etc.) was removed in a radius of 0.5 m around the stem of the selected individuals, from soil level until the top of the surrounding vegetation, so that their crowns did not interact with the surrounding vegetation any longer. Regrowing vegetation was removed monthly.

The vegetation around the other half of the individuals was left intact (‘control plants’). After 174 days biomass allocation of all individuals was determined non-destructively (they were part of another ongoing study) so that growth of control and liberated trees could be calculated (for methods and calculations on non-destructive measurements see chapter 2).

Model description

The PHOLIAGE-model is designed to calculate light absorption and photosynthetic rate of solitary trees in a vegetation stand. Here a short description of the model is given. For a detailed description and formulas see Appendix I.

We assume a tree with specific crown dimensions placed in a vegetation stand with a specific canopy height (as in Fig. 1). The length to width ratio of the crown can be varied such that vertically elongated, spherical and flatter broader crowns can be considered. The canopy of the vegetation can be fully closed and thus surround and even overtop the tree, or it can be opened up as a circular gap around the tree, thus simulating liberation. Characteristics of the tree and surrounding vegetation can be varied.

A light beam coming from any angle of the sky dome may or may not enter the surrounding vegetation before it hits the tree crown, depending on if and to what extent the canopy is opened up and on the height of the canopy. The tree crown is divided into infinitely small volume elements, approaching points. The amount of light coming from a given direction of the sky dome in a given point in the crown is calculated as a function of the path length through the crown and surrounding vegetation, their respective leaf area densities and extinction coefficients for light. This is then converted to absorbed irradiance, taking leaf absorbance and leaf angle distribution into account. The absorbed irradiance is used as input for the light response curve calculated for light saturated photosynthesis per unit volume as function of leaf nitrogen content. Subsequently integration over the sky dome gives the light absorption and photosynthesis of a given point in the crown which is then integrated over the volume of the ellipsoid to calculate whole crown light absorption and photosynthetic rate.

Light above the canopy

We assume a standard overcast sky (Goudriaan 1977). The light intensity per steradian from the sky dome (i^{Ω}_{fl}) depends on the polar angle of a light beam (ϑ_i: measured from the zenith) but is similar for light beams with different azimuth angles (measured in a horizontal plane):

$$i^{\Omega}_{fl}(\vartheta_i) = i^{\Omega}_{fl,0}(1-(\sin\vartheta_i)^c)$$

with $i_{fl,o}^{\Omega}$ the reference light intensity (from the zenith) and c the curvature type of the light-polar angle relation (in this chapter the horizontal light intensity on top of the canopy=1000 µmol m^{-2}s^{-1} and c=2).

Path length calculation

With a technique called ‘ray-tracing’ (Bartelink 2000; Pearcy and Yang 1996; Rohrig et al. 1999) we determine the path length of the beam through the crown of the tree and the surrounding vegetation by tracing it from a certain point within the crown into the direction the light is coming from (see Fig. 1 in Appendix I). Depending on the incidence angle and the gap size it will pass through the surrounding vegetation or not. If it does, it can enter the vegetation canopy either from below or from the side. By calculating the length between the point in the ellipsoid crown and the outer boundary of the crown we determine the path length of the beam through the tree's crown. We also calculate if and where the light beam enters the surrounding vegetation and the path length of the beam through the vegetation. In this way for every point in the crown and for every direction of the light beam, the path length of a beam through the crown and the vegetation can be calculated.

Light extinction

The photon flux density in a certain direction $\boldsymbol{d_i}$ must be specified in order to calculate photon absorption rate in a certain point $\boldsymbol{p}$ in the ellipsoid crown. The directional photon flux density is determined by the sky photon flux density (i_{fl}^{Ω}) from that direction (thus by the polar angle of incoming light), the light extinction coefficient (K) in that direction, the path lengths (λ) through and the leaf area density (f) of the crown (E) and the vegetation (V). The light extinction coefficient is determined by the leaf angle distribution. Leaf angles are categorized in three classes: 0-30°, 30-60° and 60-90° and are assumed to be random in the azimuth direction (Goudriaan 1988). Taking the path length through the vegetation and the crown into account, we can calculate total light extinction of a beam of any direction for any point in the crown:

$$i^{\Omega}(\mathbf{p},\mathbf{d}_i) = i_{fl}^{\Omega}(\vartheta_i)e^{-[K_E(\mathbf{d}_i)f_E\lambda_E(\mathbf{p})+K_V(\mathbf{d}_i)f_V\lambda_V(\mathbf{p})]}$$

with K_E, f_E and λ_E indicating the light extinction in the crown of the plant itself and K_V, f_V and λ_V the extinction by the surrounding vegetation.

Light absorption

The crown is divided into volume elements. The light absorption in a volume element approaches light absorption in a point when the volume element is sufficiently small. Light absorption depends on the leaf area density of a volume element and the leaf angle distribution. The light absorption rate per volume element (I_n) at point **p** in the ellipsoid crown is calculated by multiplying light absorption per unit leaf area with a certain angle (I_L), with the fraction of leaves in the same direction. This is integrated over all leaf angles (Ω_L) within each leaf angle class:

$$I_n(\mathbf{p}) = \int_{\Omega_L} f^{\Omega}(\mathbf{d}_L)I_L(\mathbf{p},\mathbf{d}_L)d\Omega_L$$

Photosynthesis

The net photosynthetic rate per unit leaf area in a point (P_L) in the ellipsoid is determined by absorbed light per unit of leaf area in that point and the nitrogen content of leaves. The light response curve is described by a non-rectangular hyperbola (Johnson and Thornley 1984):

$$p_L(I,N) = \frac{(P_{\max}(N)+\phi I)-\sqrt{(P_{\max}(N)+\phi I)^2-4\theta P_{\max}(N)\phi I}}{2\theta} - R_d(N)$$

where P_{max} is the maximum photosynthetic rate, I the absorbed photon flux, R_d the dark respiration, ϕ the quantum yield (calculated from measured values) and θ the curvature factor (set to 0.8, see Hirose et al. 1997). P_{max} and R_d are linearly related to leaf nitrogen content. We calculated the nitrogen distribution in the canopy using equation (16) proposed by Anten (1997) in which the nitrogen distribution scales with the light distribution (see also chapter 3 in which the scaling coefficient was determined for trees in a 5 y/o stand). In our model the scaling coefficient can be varied. Next the crown is divided into volume elements. Net photosynthetic rate per crown volume element (P_n) at point **p** is calculated similarly as $I_n(\mathbf{p})$:

$$P_n(\mathbf{p}) = \int_{\Omega_L} f^{\Omega}(\mathbf{d}_L) P_L(\mathbf{p}, \mathbf{d}_L) d\Omega_L$$

Whole crown photosynthesis and light absorption

Whole crown net photosynthetic rate (P_E) is calculated by integrating the net photosynthetic rate per volume element over the volume of the crown:

$$P_E = \int_{ellipsoid} P_n(\mathbf{p}) dV$$

Because integrating over an ellipsoid creates certain difficulties, the ellipsoid is transformed into a sphere. Each point and volume element in the ellipsoid is coupled to a point and volume element in a sphere. Next, an integration is made over the whole volume of the sphere:

$$P_E = abc \int_{-z}^{+z} \int_{0}^{R(z')} r' \int_{0}^{2\pi} P_n'(\mathbf{p}') d\psi' dr' dz'$$

For explanation on coordination symbols see Appendix I. Whole crown photon absorption is calculated similarly, by substituting P_E with I_E and P_n with I_n.

Model simulations

Several model calculations and simulations were done. First, we calculated whole canopy light capture and photosynthetic rates of each individual control and liberated tree immediately after removal of the vegetation in the 1.5 y/o stand (Fig. 1a). Second, we simulated the effect of an increasing gap radius in which vegetation was removed (Fig. 1a). Third, we simulated the effect of a vegetation removal event (gap radius=0.5 m) in a vegetation stand with an increasing LAI (Fig. 1b). Fourth, the effect of surrounding vegetation height was simulated in a vegetation

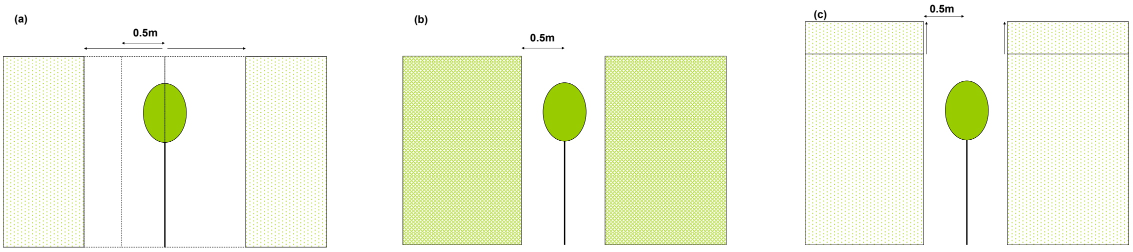

Fig. 1a-c Schematic presentation of model simulations. In Fig. 1a vegetation is removed around the individual within a variable radius, in Fig. 1b the LAI of the surrounding vegetation is increased and in Fig. 1c the vegetation height is increased (leaf area density remains constant).

removal event (gap radius=0.5 m; leaf area density of the vegetation was kept constant while height varied) (Fig. 1c). Fifth we simulated vegetation removal events with variable gap radii in three successional forest stands.

In the second, third and fourth simulation we did not consider individual trees as measured in the field. Instead, we calculated average values for tree height, crown dimensions, leaf area, leaf angle distribution and leaf nitrogen content per species based on all existing individuals of a species in the 1.5 y/o stand. Also the surrounding vegetation of the stand was averaged (LAI, height, leaf angle distribution), so that the vegetation had the same characteristics throughout the whole stand. This was done to analyse the effect of an increasing gap radius, vegetation LAI and vegetation height on species with different dimensions, leaf area and leaf nitrogen content. In the fifth simulation we digitally performed vegetation removal events with variable gap radii for individual trees within their surrounding vegetation based on actual field data as measured in chapter 2. The same individuals were liberated in three successional stands (~0.5, 1 and 1.5 y/o) of the same forest in order to determine the combined effect of tree and vegetation characteristics.

Statistical analysis

Plots were created after the slash and burn treatment with the sole purpose to be able to trace back the saplings in following measuring periods. However, in this set-up plot-effects might occur. Therefore analyses were done with Linear Mixed Effects Model (in results section abbreviated as MM).

The effect of species on the average values of light capture, photosynthetic rates and growth were determined by identifying these variables as dependent and species as factor. When designing the statistical model, species was the sole fixed effect, including intercept. For random effect an intercept was included for the subject plot number, but no model for random effects was designed. No post-hoc tests were available but most between-species differences could be deduced from the parameter estimates.

The relation between observed growth and calculated photosynthetic rate was analysed with linear regression and the difference in slopes was analysed with ANCOVA.

Results

Vegetation removal in the 1.5 y/o stand

The average height of the vegetation in the 1.5 y/o stand was 1.4 m and the LAI was on average 3.73. Species differed in height but were on average lower than the vegetation (Table 1).

Table 1 Characteristics of average trees in an average vegetation stand

Plant characteristics													Vegetation characteristics					
Species	height	leaf area	leaf angle fractions			crown vol.	crown l:w	lad	N_o	P_{max}-N_{area} relation	R_d	quantum yield	LAI	h_t	h_b	leaf angle fractions		
	(m)	(m^2)	15	45	75	(m^3)		(m^2 m^{-3})	(mmol m^{-2})	slope	(µmol $m^{-2}s^{-1}$)	(µmol $m^{-2}s^{-1}$)	(m^2 m^{-2})	(m)	(m)	15	45	75
Mallotus microcarpus	1.26	0.29	0.23	0.48	0.29	0.04	1.18	6.72	94.28	0.17	1.04	0.03	3.73	1.40	0	0.41	0.37	0.22
Mallotus paniculatus	0.94	0.06	0.13	0.41	0.46	0.01	2.00	4.94	79.33	0.10	0.24	0.03	3.73	1.40	0	0.41	0.37	0.22
Macaranga denticulata	1.07	0.11	0.37	0.40	0.24	0.03	1.42	4.35	82.52	0.18	0.53	0.04	3.73	1.40	0	0.41	0.37	0.22

Note: values are calculated based on individuals and vegetation characteristics in the 1.5 y/o stand (data were taken from chapter 2). Leaf angle fractions are divided into three classes indicated by 15, 45 and 75 degrees, crown l:w is the ratio between the length and the width of the crown, lad is leaf area density, No is maximum nitrogen content of the leaves, Rd is dark respiration, ht and hb are top height resp. bottom height of the vegetation. Photosynthesis data are taken from chapter 2

Model calculations showed that in all species liberated individuals on average tended to have higher absolute whole canopy light capture rates (µmol s^{-1}) (the horizontal light intensity on top of the canopy was set to 1000 µmol $m^{-2}s^{-1}$) and photosynthetic rates (µmol s^{-1}) immediately after removal of vegetation than the control individuals (Fig. 2a-b) but none of these differences were significant (MM, p>0.05). Liberated plants had significant higher light capture per unit of leaf area (Φ_{area}) and photosynthetic rate per unit of leaf area (P_{area}) (Fig. 2c-d) (MM, p<0.05) than control plants, except for P_{area} of *Mallotus microcarpus* (MM, p=0.133).

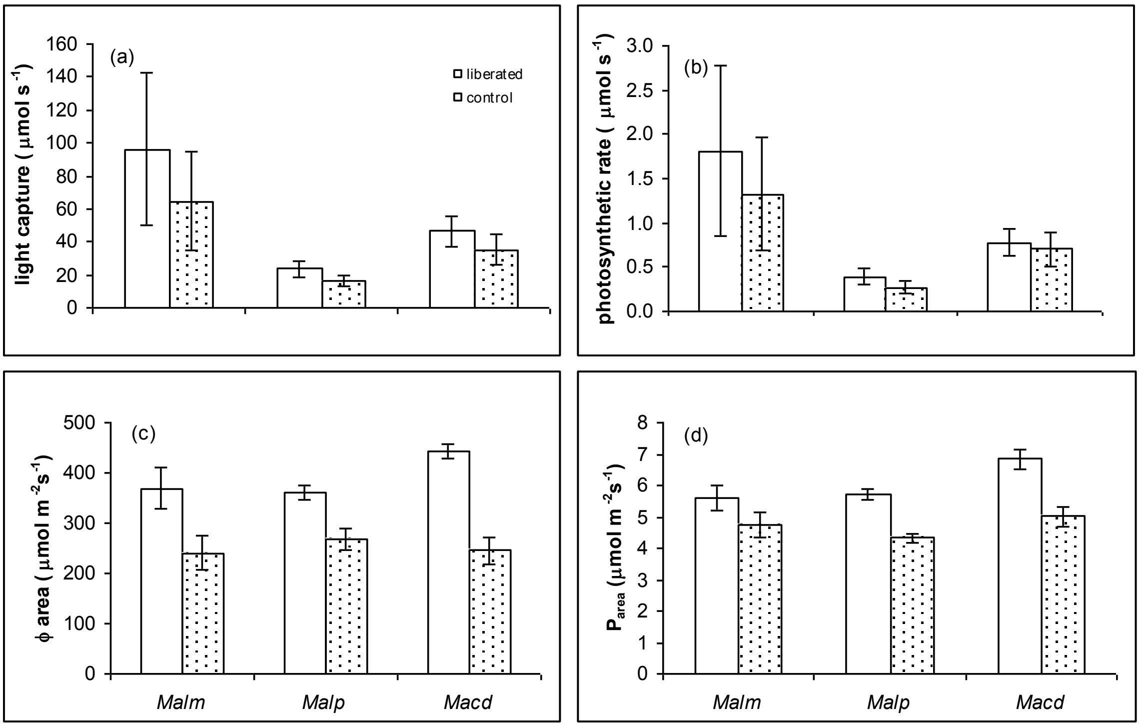

Fig. 2a-d Mean values of whole canopy light capture and photosynthetic rate of control and liberated plants immediately after vegetation removal (gap radius=0.5 m) in a 1.5 y/o secondary forest stand in Vietnam (the horizontal light intensity on top of the canopy was set to 1000 µmol $m^{-2}s^{-1}$). Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata*. Bars denote standard error.

Above ground Relative Growth Rate (RGR) and relative height growth rate were determined in the period following the removal of the surrounding vegetation (Fig. 3). Vegetation removal tended to result in a higher RGR (Fig. 3a), but this was only significant for *Mallotus paniculatus* (MM, p=0.043). Height growth tended to be lower for liberated plants (Fig. 3b), but this was only significant for *Macaranga denticulata* (MM, p=0.036).

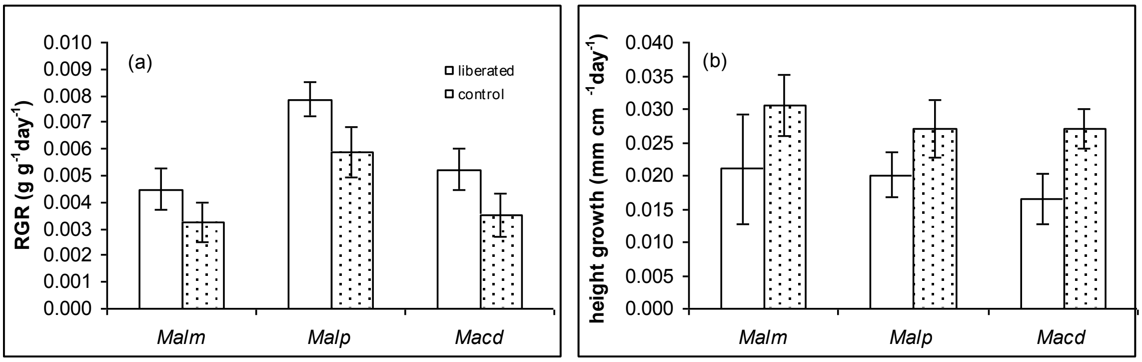

Fig. 3a-b Above ground Relative Growth Rate (RGR) and relative height growth rate of control and liberated plants in 174 days after vegetation removal (gap radius=0.5 m). Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata*. Bars denote standard error

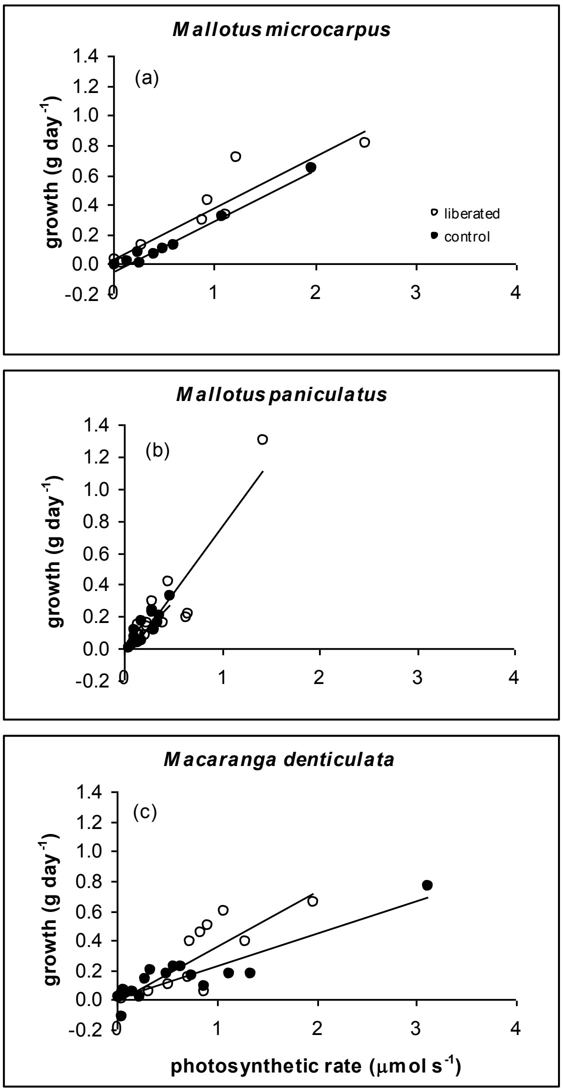

Fig. 4a-c Correlation between observed above ground biomass growth in 174 days after vegetation removal and calculated whole canopy photosynthetic rates immediately after vegetation removal. All correlations are significant (MM, $p<0.01$) and r^2 values varied from 0.6928 to 0.9744.

Model calculations of instantaneous absolute photosynthetic rates immediately after removal of vegetation, were correlated to above ground mass growth (g day^{-1}) in the period following removal (Fig. 4). All species showed significant positive correlations for the control and the liberation treatment. Within a species slopes between treatments were similar (MM, $p>0.05$). Slopes were higher for *Mallotus paniculatus* than for the other species (MM, $p=0.011$). *Mallotus paniculatus* had relatively low dark respiration (Table 1) which might be related to the higher slope.

Model simulation: variation in gap radius

The characteristics of the average trees and the average stand are given in Table 1. The simulated effects of vegetation removal in an increasing gap radius on light capture and photosynthetic rate of the target trees are depicted in Fig. 5.

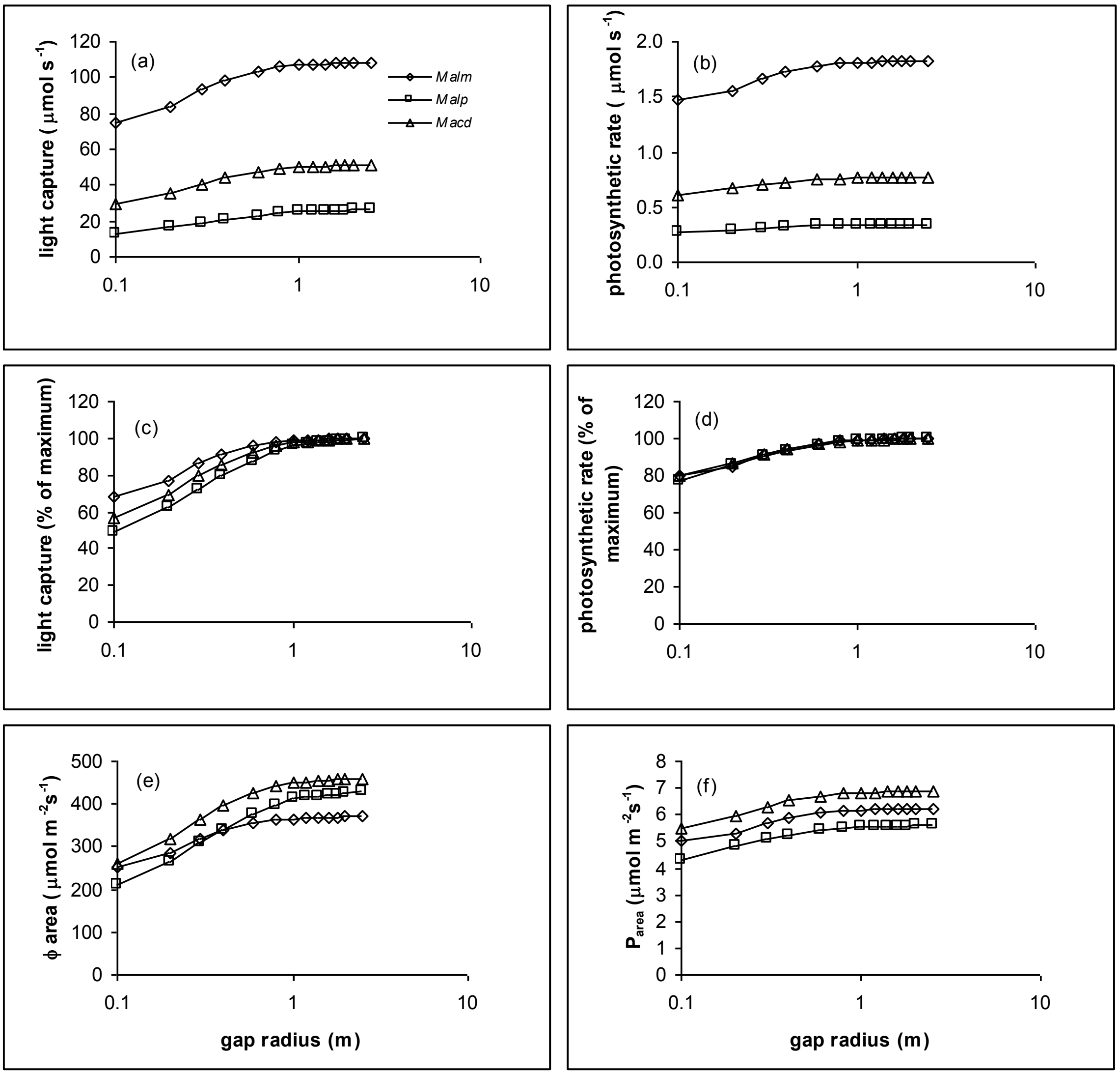

Fig. 5a-f Model simulations of the effect of gap radius on whole canopy light capture and photosynthetic rate of species in a 1.5 y/o secondary forest stand. Mean parameter values were used for each species and treatment. Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata*.

Values of absolute light capture and photosynthetic rates increased with increasing gap radius and reached near-maximum values at a gap radius of approximately 1 m (Fig. 5a-b). *Mallotus microcarpus* captured the largest amount of light and had highest photosynthetic rate while *Mallotus paniculatus* captured the least light and had the lowest photosynthetic rate. This corresponded with species height and leaf area (Table 1). *Mallotus microcarpus* was the tallest species, the top of its crown reached on average 90% of the surrounding vegetation height, and it had the most leaf area. *Mallotus paniculatus* was the shortest species with a mean height of 67% of the surrounding vegetation height, and it had the smallest leaf area. *Macaranga denticulata* showed intermediate values for light capture, photosynthetic rates, height and leaf area.

Fig. 5c shows that *Mallotus microcarpus* reached maximum values of light capture (as percentage of light capture at a gap radius of 2.5 m) before the other species did. This was related to the crown shape of the species and species height. *Mallotus microcarpus* had the smallest crown length compared to its crown width (Table 1) and it was positioned relatively high in the canopy. Thus with increasing gap radius, the bottom part of its crown will be capturing maximum light levels sooner than a crown that is placed lower in the vegetation and has a longer crown length compared to its width like that of *Mallotus paniculatus* (Fig. 6). *Macaranga denticulata* had an intermediate crown size and was positioned at intermediate height in the vegetation and the simulation line in Fig. 5c fell between that of the other species.

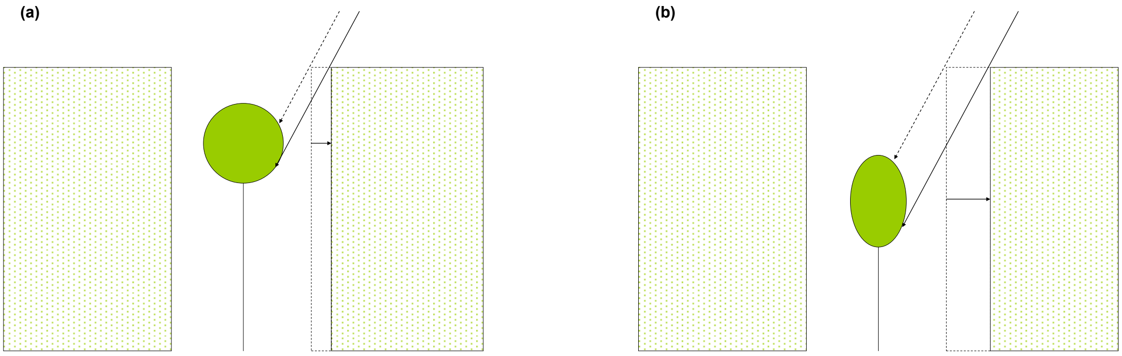

Fig. 6a-b Schematic presentation of the effect of vegetation removal on light capture of trees with different crown position and crown shape: a spherical shaped crown high in the canopy (a) versus an elongated crown lower in the canopy (b).

Photosynthetic rate as percentage of the maximum photosynthetic rate was approximately equal for all species at all gap radii (Fig. 5d). The discrepancy between Fig. 5c and 5d can be explained by the photosynthetic characteristics of the species (Table 1). *Mallotus microcarpus* could achieve high levels of maximum photosynthetic rates (high N_o and high slope of the P_{max}-N_{area} relation) and had a high dark respiration (R_d). *Mallotus paniculatus* on the other hand was not able to achieve such high levels of maximum photosynthetic rates and its dark respiration was low, which is favorable in low light conditions. *Macaranga denticulata* could also achieve relatively high maximum photosynthetic rates and had intermediate R_d. Thus the tallest species, *Mallotus microcarpus,* was most able to keep up with the surrounding vegetation height, but was also most light-demanding.

With increasing gap radius, Φ_{area} increased for all species (Fig. 5e). The lower increase of *Mallotus microcarpus* can be explained by its relatively short crown and is position high in the canopy. Many leaves already experience high light levels thus an increase in gap radius will increase Φ_{area} but not as much as for a tree with a more elongated crown positioned lower in the canopy. The relatively low value of maximum Φ_{area} for *Mallotus microcarpus* is the consequence of its higher leaf area density compared to the other species (Table 1). This increases self-shading.

Mallotus paniculatus had the lowest mean photosynthetic rate per unit leaf area (Fig. 5f). This related to its relatively low maximum photosynthetic rate. *Macaranga denticulata* showed the highest P_{area} because of its high maximum photosynthetic rates and high Φ_{area}.

Model simulation: variation in LAI and vegetation height

The effect of LAI of the surrounding vegetation on photosynthetic rates of the average trees for both the control and the liberated plants is shown in Fig. 7 (for average vegetation characteristics see Table 1). When the surrounding vegetation was left intact, photosynthetic rates declined with increasing LAI for all species (Fig. 7a). The decline was steepest for the species highest in the canopy, *Mallotus microcarpus,* because in absolute terms light availability diminishes more strongly higher in the canopy than lower down and this species had higher respiration. When vegetation was removed around the individual trees in a radius of 0.5 m, its LAI hardly influenced photosynthetic rates (Fig. 7b).

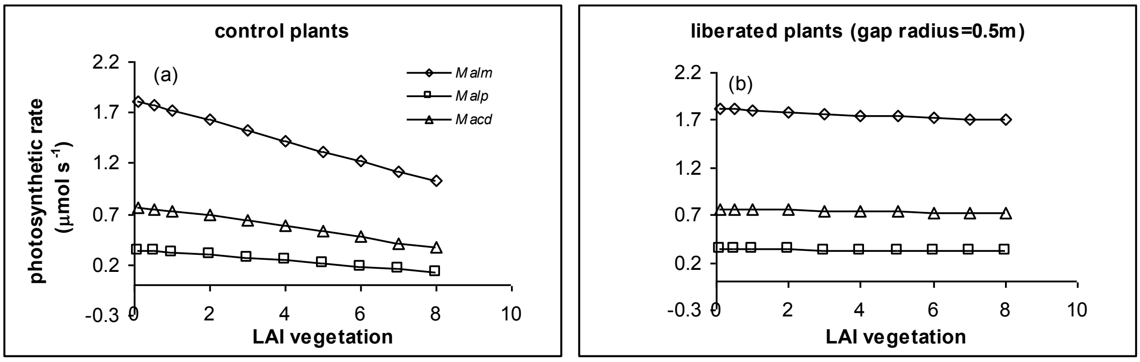

Fig. 7a-b Model simulations of the effect of LAI of the surrounding vegetation on whole canopy photosynthetic rates of species in a control situation (surrounding vegetation intact) (a) and liberated plants (b) in a 1.5 y/o secondary forest stand. Mean parameter values were used for each species and treatment. Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata*.

The effect of height of the surrounding vegetation on photosynthetic rates of the average trees for both the control and the liberated plants is shown in Fig. 8. When vegetation height was increased (for average vegetation characteristics see Table 1), photosynthetic rates declined in the control and the liberation treatment, but the effect for the control plants 5was stronger than for the liberated plants. *Mallotus microcarpus* reached negative photosynthesis values before the other species did. The sudden decline in photosynthetic rate indicated the moment the height of the surrounding vegetation exceeded that of the target trees.

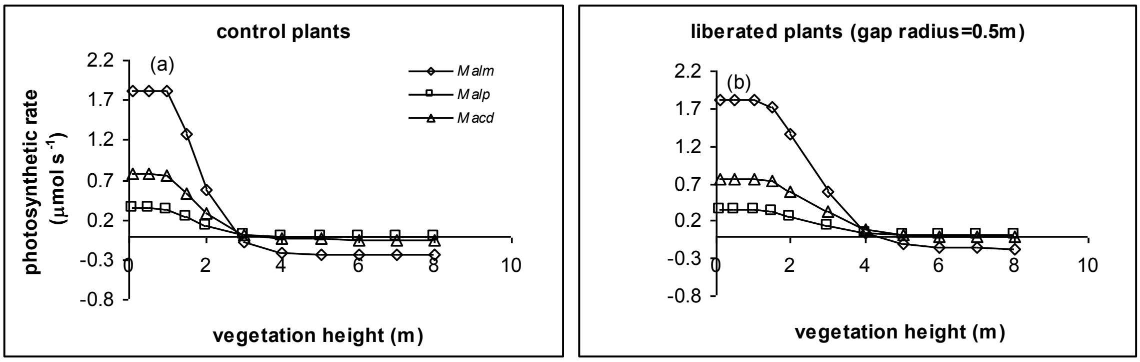

Fig. 8a-b Model simulations of the effect of height of the surrounding vegetation on whole canopy photosynthetic rates of species in a control situation (surrounding vegetation intact) (a) and liberated plants (b) in a 1.5 y/o secondary forest stand (LAI was changed with vegetation height so that leaf area density remained constant). Mean parameter values were used for each species and treatment. Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata*.

Model simulation: vegetation removal in successional stands

The average response of all individuals of a species to a vegetation removal event with different gap radius in three successional stands of the same forest (Table 2) is shown in Fig. 9. In all stands and for all species photosynthetic rate (as a percentage of photosynthetic rate in the control situation: gap radius=0 m) increased with increasing gap radius. In the 1.5 y/o stand the effect of vegetation removal was not as great as in the 1 and 0.5 y/o stands. In the 1.5 y/o stand trees were on average closer to the top of the vegetation than in the younger stands (see chapter 2). Thus average photosynthetic rates in the 1.5 y/o stand were closer to the maximum values than in the same individuals in the younger stands.

Table 2 Characteristics of successional vegetation stands in a Vietnamese forest

	Stand I	Stand II	Stand III
age (yr)	~0.5	~1	~1.5
mean LAI (m^2m^{-2})	3.03+/-1.74	5.46+/-0.91	3.73+/-0.75
mean height (m)	0.61+/-0.18	0.99+/-0.31	1.4+/-0.41

Note: data are taken from chapter 2

In the 1 y/o stand (Fig. 9b) it seems as if vegetation removal affected photosynthetic rates of *Mallotus microcarpus* less than those of *Mallotus paniculatus* and *Macaranga denticulata*. In the 0.5 y/o stand (Fig. 9c) the opposite seemed to occur. In the 0.5 y/o stand all species had approximately the same height respective to the vegetation height (results not shown). *M. microcarpus* had a two-fold higher leaf area and a lower leaf area density than the other species (results not shown), resulting in a higher potential photosynthetic rate. In the 1 y/o stand *M. microcarpus* had the highest height respective to the vegetation height (results not shown), so it was closer to maximum levels of photosynthesis than the other species. Therefore an increase in gap radius had less effect.

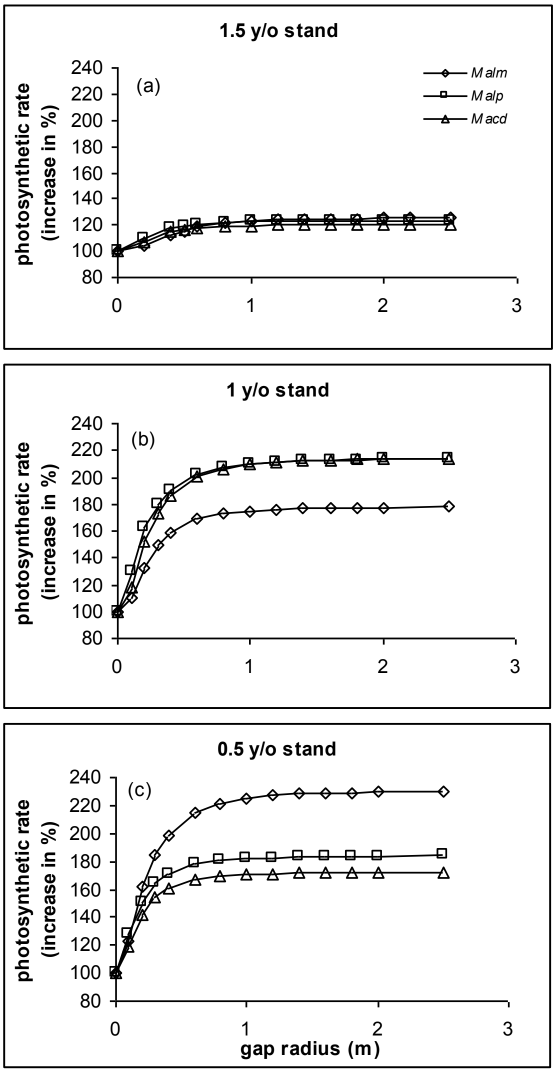

Fig. 9a-c Model simulations of the effect of gap radius on whole canopy photosynthetic rates of species in three successional vegetation stands of the same forest. Simulations were done for individual trees (data were taken from chapter 2). Abbreviations: *Malm, Mallotus microcarpus; Malp, Mallotus paniculatus; Macd, Macaranga denticulata*.

When calculating the increases in photosynthetic rates as percentage of the maximum photosynthetic rates (at a gap radius of 2.5 m), differences between species and stands were small (90-96% with a gap radius of 0.5 m and 98-99% with a gap radius of 1 m, depending on species and stand).

Discussion

Removing surrounding vegetation around target trees in a young secondary forest stand was calculated to be beneficial in terms of light capture and photosynthetic rate. The species in this study responded differently to the treatment depending on their morphological and physiological characteristics. The responses were also strongly dependent on the characteristics of the surrounding vegetation. There were strong correlations between calculated photosynthetic rates and observed growth, indicating that the model presented in this paper was well able to predict the growth of trees in early successional forests and the effects of a commonly used practice, removal of surrounding vegetation, there upon.

In the 1.5 y/o stand vegetation removal in a gap radius of 0.5 m resulted in higher light capture and higher photosynthetic rate per unit leaf area and a tendency towards higher biomass growth and reduced height growth of the trees as compared to the trees in the control situation. Similar results were obtained by Collet et al. (1998) in an oak plantation. They related differences in stem allometry to the effect of shade produced by the surrounding vegetation, or reduction thereof which decreases the need to grow tall (see also Guariguata 1999). Differences in growth were according to them the result of the reduction of belowground competition between neighboring plants and the target trees. In our study this reasoning may hold but we argue that higher biomass growth of the liberated trees certainly also was a result of increased light levels.

Near-maximum values of light capture and photosynthetic rates were reached at a gap radius of approximately 1 m. Additional cutting in a bigger radius would hardly increase light capture and photosynthetic rates. Ådjers et al. (1995) found that planted trees showed no additional growth in strips wider than 2 m in a 3 m high tropical forest. The radius (or width in case of a strip) at which near maximum light levels for growth are reached depends on the vegetation height relative to that of the target tree and thus will be different for every forest stand (Ådjers et al. 1995; Pena-Claros et al. 2002). The optimal radius for any stand can be determined with the model presented here.

The degree to which light capture of plants increased with increasing gap radius differed considerably between species. This could be related to interspecific differences in morphological traits such as leaf area, tree height (i.e. the crown’s position in the canopy) and crown dimensions. Crown architecture determines the display of leaves, light interception, and thus carbon acquisition (Bongers and Sterck 1998). In our study leaf area density appeared to influence light capture per unit leaf area. A high leaf area density results in self-shading within the crown and this reduces light capture. Shaded leaves do not necessarily have negative carbon balances but self-shading does lower whole plant carbon gain (Pearcy and Yang 1996; Sterck et al. 2003). Differences in physiological traits between species explained the course of the photosynthetic rate with increasing gap radius, increasing LAI and increasing height. *Mallotus paniculatus* plants had lower photosynthetic capacities but also lower rates of dark respiration than the other species, and this favored their net carbon gain at low, but not at high light. Thus while this species exhibited a great increase in light capture per unit leaf area, it did not similarly show a great increase in net photosynthesis.

Above mentioned results show that as was found by others, species, even the closely related ones, differ in their optimal light conditions (Ådjers et al. 1995; Dupuy and Chazdon 2006; Montagnini et al. 1997; Ramos and del Amo 1992). In our study it appeared that the species that was most able to keep up with the vegetation height was the most light-demanding one. Slower growing species grow in increasingly darker environments since they lack the ability to grow tall rapidly, however, they are also less light-demanding and respond less strongly to increasing light levels. This could result in equal effects of increasing gap radius for species with different light requirements (see Fig. 9a) growing at different light levels.

Vegetation removal experiments in forests generally result in increased growth of the liberated trees (Collet et al. 1998; Finegan et al. 1999) but they have not always been successful because in some cases vegetation surrounding trees appeared to facilitate tree recruitment by changing soils conditions (Aide et al. 1996; Li et al. 1999; Vieira et al. 1994). The degree of success of a vegetation removal event depends on many factors such as site characteristics (soil moisture content and nutrient availability) (Li et al. 1999; Putz and Canham 1992), the light requirement of the target species (Dupuy and Chazdon 2006; Petritan et al. 2007), the type of plants in the surrounding vegetation (Holl 1998; Vieira et al. 1994), the number of removal events (De Graaf et al. 1999; Pariona et al. 2003) and the timing of the intervention (Fuhr et al. 2001). We demonstrated that our model can provide insight into the effects of vegetation removal and how this depends on the characteristics of the target species and the vegetation, the radius in which vegetation is removed and the timing of removal events. For this specific forest we showed that the greatest effects of vegetation removal are resorted if the vegetation is removed in the 0.5 or the 1 y/o stand rather than in the 1.5 y/o stand. When we compare the effects of a gap radius of 0.5 m versus a gap radius of 1 m we hardly see additional gains in photosynthetic rates but it will cost a lot more labor, and thus money, to create a gap with a larger radius. Thus a gap radius of 0.5 m seems appropriate here. Even though factors such as soil and climate characteristics are not incorporated in the model, the simulation of vegetation removal in different successional stands is an appropriate practical example that shows the potential use of the model for decisions in the field.

Obviously costs are involved when vegetation removal events are performed (McNamara et al. 2006; Montagnini et al. 1997). The model presented here seems to make good qualitative predictions of the effects of vegetation removal on tree growth and as such it is useful in planning vegetation removal events that are productive in terms of tree growth and economically feasible. In the case of commercial species being liberated (De Graaf et al. 1999; Guariguata 1999), costs of liberation will eventually be returned by the profit of selling increased quantities of timber (Pariona et al. 2003; Wadsworth and Zweede 2006).

Many field experiments on vegetation removal have been done but they require a lot of time, space and money and results are restricted to a particular situation and generally cover limited amounts of experimental conditions and replication (Paquette et al. 2006). With the model approach presented here we can simulate vegetation removal events in different scenarios and as such it provides a useful tool in planning liberation activities.

Appendix I

PHOLIAGE-model description

A short description of the PHOLIAGE-model is given in the Methods section. Here the model is described in detail. First it is explained how integration over an ellipsoid crown is done in order to calculate whole crown light absorption and photosynthetic rate. Next we explain how the photosynthetic rate per volume element of the crown is calculated and how this is determined by light absorption in the volume element and leaf nitrogen content. Finally we show how the light intensity for each point in the crown can be found by ray-tracing. Here path lengths of the light beam through the crown and the surrounding vegetation are taken into account. It should be noted that in this appendix we use a different argumentation than the one in the Methods section. Here we start with how the total photosynthetic rate of the plant is to be interpreted as a sum (an integral) of rates over the crown, and end with a formalisation of the light coming from the sky.

The model tree and its surrounding vegetation

We assume a target tree with an ellipsoid shaped crown placed in a vegetation stand (see Fig. 1 in Methods). All positions in and around the ellipsoidal crown are given in terms of Cartesian coordinatisation, with the origin in the centre of the ellipsoid. The shape of the ellipsoid is characterised by the lengths of the semi-axes a, b and c in the x-, y- and z-direction, with the z-axis pointing towards the zenith.

The tree crown is surrounded by vegetation with infinite horizontal extensions. The vertical dimensions of the vegetation are given by top height h_t and bottom height h_b. The tree and the surrounding vegetation are completely separated in terms of leaf distribution. The vegetation around a target tree can be opened up as a cylinder with the z-axis of the cylinder coinciding with the z-axis of the ellipsoid. The radius of the cylinder (r_{gap}) can have any non-negative value and is not limited by the a- or b-axes of the ellipsoid. The top and bottom positions of the ellipsoid (with $z=-c$ and $z=c$) can have any position with respect to the surrounding vegetation. For both the crown and the surrounding vegetation, leaf area density and leaf angle distribution are assumed to be homogeneous.

Whole crown photosynthetic rate and photon absorption rate

The net whole crown photosynthetic rate is calculated by integrating the net photosynthetic rate per unit volume over the crown. P_n denotes the net photosynthetic rate per unit volume at a point

p within the ellipsoidal crown. The total net photosynthetic rate of the crown P_E (in µmol s^{-1}) is given by the integral:

$$P_E = \int_{ellipsoid} P_n(\mathbf{p})dV \tag{1}$$

To simplify the integration the ellipsoid is related to a unit sphere, meaning that every point **p**' in the unit sphere is related to a point **p** in the ellipsoid by:

$$(p_x,p_y,p_z) = (ap'_x,bp'_y,cp'_z) \tag{2}$$

The photosynthetic rate per unit volume P_n'(**p**') in the unit sphere is related to the photosynthetic rate P_n(**p**) in the associated ellipsoid by:

$$\mathbf{p}' \to P_n'(\mathbf{p}') = P_n(ap'_x,bp'_y,cp'_z) = P_n(\mathbf{p}) \tag{3}$$

For the net crown photosynthetic rate we now find:

$$P_E = abc \int_{sphere} P_n'(\mathbf{p}')dV' \tag{4}$$

When expressing the Cartesian coordinates in terms of cylindrical coordinates this results in:

$$P_E = abc\int_{-z}^{+z}\int_{0}^{R(z')} r' \int_{0}^{2\pi} P_n'(\mathbf{p}')d\psi'dr'dz' \tag{5}$$

with

$$\mathbf{p}' = (r'\cos\psi', r'\sin\psi', z')$$

$$R(z') = \sqrt{1-z'^2}$$

and

$$z' \in (-1,1)$$

Net crown photon absorption rate is calculated similarly, by substituting P_E with I_E and P_n with I_n (for P_n and I_n see next sections).

Photosynthetic rate per unit volume

Net photosynthetic rate per unit crown volume P_n (µmol $m^{-3}s^{-1}$) is calculated by integrating the product of net photosynthetic rate per unit leaf area for leaves with normal $\mathbf{d}_L$ and the fraction of the total leaf area in direction $\mathbf{d}_L$ per steradian f^{Ω}, over all positive (faced upwards) leaf angles Ω_L (steradian):

$$P_n(\mathbf{p}) = \int_{\Omega_L} f^{\Omega}(\mathbf{d}_L)P_L(\mathbf{p},\mathbf{d}_L)d\Omega_L \tag{6a}$$

Using spherical coordinates, P_n(**p**) can be written as:

$$P_n(\mathbf{p}) = \int_{0}^{\frac{\pi}{2}} \sin\vartheta_L f^{\Omega}(\vartheta_L)\int_{0}^{2\pi} P_L(\mathbf{p},\vartheta_L,\psi_L)d\psi_L d\vartheta_L \tag{6b}$$

in which f^{Ω} is assumed to be independent of the azimuth angle and leaf normals are assumed to be directed into the upper hemisphere.

Net photosynthetic rate per unit leaf area P_L (µmol $m^{-2}s^{-1}$) in point **p** for light direction **d** is calculated from net photosynthetic rate per unit leaf area p_L which is a function of net photon absorption rate per unit leaf area I_L and leaf nitrogen content N:

$$P_L(\mathbf{p},\mathbf{d}_L) = p_L(I_L(\mathbf{p},\mathbf{d}_L), N(\mathbf{p})) \tag{7}$$

Net photosynthetic rate

Net photosynthetic rate per unit leaf area (µmol $m^{-2}s^{-1}$) is characterised by a non-rectangular hyperbola (Johnson and Thornley 1984):

$$p_L(I,N) = \frac{(P_{\max}(N) + \phi I) - \sqrt{(P_{\max}(N) + \phi I)^2 - 4\theta P_{\max}(N)\phi I}}{2\theta} - R_d(N) \tag{8}$$

where P_{max} is the maximum photosynthetic rate (µmol m^{-2} s^{-1}) and ϕ and θ are the quantum yield (mol mol^{-1}) and the curvature of the photosynthesis curve, respectively. P_{max} is assumed to be a curvilinear function of leaf N content:

$$P_{\max}(N) = \frac{(a_p N + b_p)c_p}{(a_p N + b_p) + c_p} \tag{9a}$$

If this relation is assumed to be linear (depending on the measuring method) the asymptote is set to ∞, and eq.(9a) converges to:

$$P_{\max}(N) = a_p N + b_p \tag{9b}$$

Dark respiration R_d (µmol $m^{-2}s^{-1}$) is given by:

$$R_d(N) = a_R N + b_R \tag{10}$$

Nitrogen distribution

The leaf nitrogen content $N(\mathbf{p})$ (mmol m^{-2}) at any point **p** in the crown is characterised by an empirical relation between light attenuation and nitrogen distribution (Anten 1997):

$$N(\mathbf{p}) = N_0 \left(\frac{I(\mathbf{p})}{I_0} \right)^{a_N} \tag{11}$$

where N_0 is the N content of a fully illuminated leaf in the top of the crown and a_N indicates the coefficient with which the nitrogen distribution scales with the light distribution. $I(\mathbf{p})$ is the photon flux density at point p, characterised as $I_n(\mathbf{p})/a_L$ (see next section) and I_o is $I(p)$ at the top of the crown (**p**=0,0,*c*). Note that varying a_N-values result in a change in the total nitrogen content of the crown.

Photon absorption rate per unit volume

The photon absorption rate per unit volume I_n (µmol m^{-3}s^{-1}) is given by the integral:

$$I_n(\mathbf{p}) = \int_{\Omega_L} f^{\Omega}(\mathbf{d}_L) I_L(\mathbf{p},\mathbf{d}_L) d\Omega_L \tag{12a}$$

When rewriting this formula to spherical coordinates we get:

$$I_n(\mathbf{p}) = \int_0^{\frac{\pi}{2}} \sin\vartheta_L f^{\Omega}(\vartheta_L) \int_0^{2\pi} I_L(\mathbf{p},\vartheta_L,\psi_L) d\psi_L d\vartheta_L \tag{12b}$$

So the photon absorption rate per unit volume is determined by both the leaf area density and f^{Ω} in direction $\mathbf{d}_L$ and the net photon absorption rate I_L per unit leaf area (µmol m^{-2}s^{-1}) for leaves with leaf normal $\mathbf{d}_L$, which is:

$$I_L(\mathbf{p},\mathbf{d}_L) = a_L \int_{\Omega_i} \left|\langle \mathbf{d}_L,\mathbf{d}_i \rangle\right| i^{\Omega}(\mathbf{p},\mathbf{d}_i) d\Omega_i \tag{13a}$$

or

$$I_L(\mathbf{p},\mathbf{d}_L) = a_L \int_0^{\frac{\pi}{2}} \sin(\vartheta_i) \int_0^{2\pi} \left|\langle \mathbf{d}_L(\vartheta_L,\psi_L),\mathbf{d}_i(\vartheta_i,\psi_i) \rangle\right| i^{\Omega}(\mathbf{p},\vartheta_i,\psi_i) d\psi_i d\vartheta_i \tag{13b}$$

Here $|\langle\mathbf{d}_L,\mathbf{d}_i\rangle|$ is the magnitude of the inner product $\langle\mathbf{d}_L,\mathbf{d}_i\rangle$ of the leaf normal $\mathbf{d}_l$ and the unit length light direction vector $\mathbf{d}_i$. Symbol i^{Ω} denotes the light intensity per steradian coming from direction $\mathbf{d}_i$ and a_L is the leaf light absorption coefficient.

Photon flux density

To calculate the photosynthetic rate or the photon absorption rate for any point in the crown, the spherical light distribution must be specified. This directional photon flux density is determined by the extinction coefficient in that direction, the path lengths through the crown and the surrounding vegetation and the sky photon flux density for that direction.

Extinction coefficient and light attenuation

In general, the light attenuation through vegetation can be expressed as a differential equation of photon flux density per steradian from direction $\mathbf{d}_i$ over path length λ through the vegetation:

$$\frac{di^{\Omega}(\mathbf{d}_i)}{d\lambda} = -K(\mathbf{d}_i) f i^{\Omega}(\mathbf{d}_i) \tag{14}$$

where the product of the light extinction K and the leaf area density f (m^2 m^{-3}) is a function of the projection of all leaves in direction $\mathbf{d}_i$ multiplied by the leaf light absorption coefficient a_L:

$$K(\mathbf{d}_i) f = a_L \int_{\Omega_L} \left|\langle \mathbf{d}_L,\mathbf{d}_i \rangle\right| f^{\Omega}(\mathbf{d}_L) d\Omega_L \tag{15a}$$

or

$$K(\mathbf{d}_i)f = a_L \int_0^{\frac{\pi}{2}} \sin(\vartheta_L) f^{\Omega}(\vartheta_L) \int_0^{2\pi} \left| \langle \mathbf{d}_L(\vartheta_L,\psi_L), \mathbf{d}_i(\vartheta_i,\psi_i) \rangle \right| d\psi_L \, d\vartheta_L \tag{15b}$$

(Note that leaf area density per steradian f^{Ω} is independent of the azimuth angle.)
Solving eq.(14) results in a general expression for the directional light intensity:

$$i^{\Omega}(\mathbf{d}_i,\lambda) = i^{\Omega}_{fl}(\mathbf{d}_i) e^{-K(\mathbf{d}_i)f\lambda} \tag{16}$$

where i^{Ω}_{fl} is the free sky light intensity per steradian (µmol $m^{-2}s^{-1}sr^{-1}$), f the leaf area density and λ the path length through the vegetation. Because the surrounding vegetation (index V) and the plant's crown (index E) may have different leaf area densities and leaf normal distributions, they may have different extinction coefficients. Eq.(16) should therefore be rewritten as:

$$i^{\Omega}(\mathbf{p},\mathbf{d}_i) = i^{\Omega}_{fl}(\vartheta_i) e^{-[K_E(\mathbf{d}_i)f_E\lambda_E(\mathbf{p}) + K_V(\mathbf{d}_i)f_V\lambda_V(\mathbf{p})]} \tag{17}$$

Leaf area density

The leaf area density f (m^2m^{-3}) in terms of the leaf normal distribution at any point in the ellipsoid is given by the integral:

$$f = \int_{\Omega_L} f^{\Omega}(\mathbf{d}_L) d\Omega_L \tag{18}$$

To calculate the leaf area density distribution per steradian f^{Ω} (m^{-3}) from field data the total leaf area density f is split up and measured in a number of classes:

$$f = f_1 + f_2 + \ldots + f_n = f(f'_1 + f'_2 + \ldots + f'_n)$$

Here f'_k is the fraction of the total leaf area density with a normal in polar directions θ_k. For each direction class the density per steradian f^{Ω}_k is assumed to be uniform. Consequently, for each direction class k:

$$f^{\Omega}_k = \frac{f \cdot f'_k}{A_k} \tag{19}$$

with A_k the area on the unit sphere associated with the direction class k. The classes are defined by splitting the polar angle interval (0,2π) into intervals of equal width:

$$A_k = 2\pi(\cos\vartheta_{k-1} - \cos\vartheta_k) \tag{20}$$

with θ_k and θ_{k-1} the upper and lower bounds of interval k.

This division in classes makes f^{Ω} a non-continuous function. Consequently, in the numerical implementation the Gaussian integration over the azimuth angle ($d\theta$) of functions (15b) and (13b) is done separately over each leaf normal class.

Path lengths

The extinction of a light beam with direction $\mathbf{d}_i$ is determined by the path length of the beam through the crown and the surrounding canopy (Fig. 1).

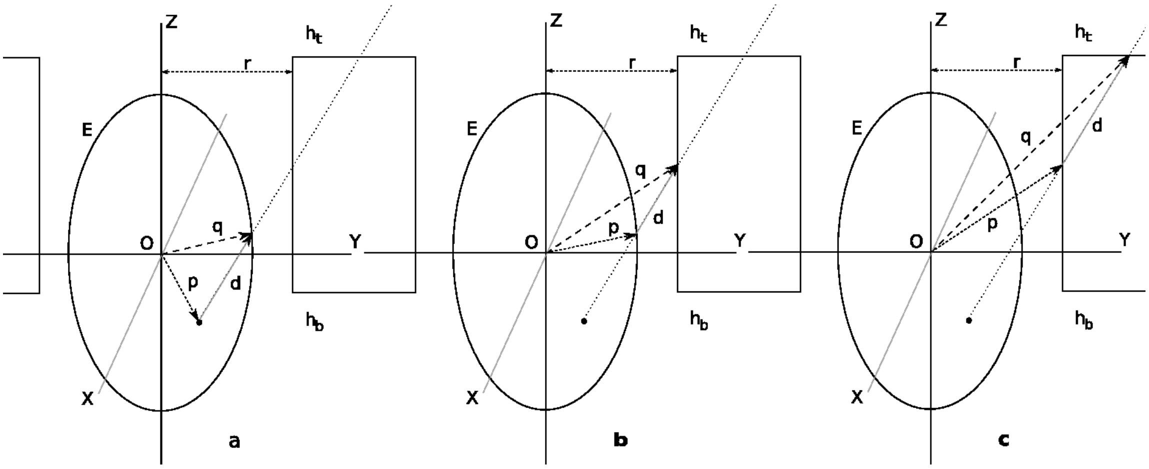

Fig. 1 Three sets of vectors are used for path length calculations through crown (a), gap space (b) and surrounding vegetation (c).

Path length through the crown

Vector $\mathbf{p}=(p_x, p_y, p_z)$ denotes a vector to a point in the interior of the ellipsoid and vector $\mathbf{d}=(d_x, d_y, d_z)$ is a unit length vector specifying the direction for which the directional light intensity has to be calculated (Fig. 1a). The length of the vector $\mathbf{p}$ to a point $\mathbf{q}$ on the boundary ∂E of the ellipsoid, pointing in direction $\mathbf{d}$, is written as $\lambda\mathbf{d}$. Since vector $\mathbf{d}$ has unit length, λ is the path length of the light beam through the tree crown. The directional path from $\mathbf{p}$ to point $\mathbf{q}$ can be parameterised by:

$$\mathbf{q}(\lambda)=\mathbf{p}+\lambda\mathbf{d} \tag{21}$$

with $\lambda\geq 0$. For the point of intersection $\mathbf{q}(\lambda)$ of this path with the boundary ∂E of the ellipsoid we get:

$$\frac{(q_x(\lambda))^2}{a^2}+\frac{(q_x(\lambda))^2}{b^2}+\frac{(q_x(\lambda))^2}{c^2}=1 \tag{22}$$

Expansion of this equation results in a quadratic expression for path length λ:

$$\alpha\lambda^2+\beta\lambda+\gamma=0 \tag{23}$$

with:

$$\alpha=\frac{{d_x}^2}{a^2}+\frac{{d_y}^2}{b^2}+\frac{{d_z}^2}{c^2}$$

$$\beta=\frac{2d_x p_x}{a^2}+\frac{2d_y p_y}{b^2}+\frac{2d_z p_z}{c^2}$$

$$\gamma=\frac{{p_x}^2}{a^2}+\frac{{p_y}^2}{b^2}+\frac{{p_z}^2}{c^2}-1$$

(Note that we are only interested in the positive root of this equation.)

Path length through the surrounding vegetation

Part of the path from **p** in direction **d** might be passing through the surrounding vegetation. Whether this is the case depends on the parameter values for the crown, gap radius and height of the surrounding vegetation. To illustrate the calculation of the path length of a light beam that passes through the vegetation, a sufficiently high vegetation is assumed with a gap having a radius that is larger than the semi-axes *a* and *b* of the crown.

To calculate the path length in direction **d** for a point **p** on the boundary ∂E of the ellipsoid through the free space between the crown and the vegetation (Fig. 1b), the path is again described by an expression as given in eq.(21). For the point of intersection with the cylindrical gap side boundary we get:

$$(q_x(\lambda))^2 + (q_y(\lambda))^2 = r^2 \tag{24}$$

Expansion results in a quadratic expression for λ:

$$\alpha\lambda^2 + \beta\lambda + \gamma = 0 \tag{25}$$

with:

$$\alpha = {d_x}^2 + {d_y}^2$$

$$\beta = 2p_x d_x + 2p_y d_y$$

$$\gamma = {p_x}^2 + {p_y}^2 - r^2$$

where λ is specified by the positive root of the equation.

The coordinate q_z determines whether the point of entry in the vegetation will be in the cylinder side boundary or in the vegetation bottom boundary. In this illustration, the point of intersection is in the cylinder side and consequently $h_b < q_z(\lambda) < h_t$.

To calculate the path length through the vegetation, a point **p** lying on the side boundary of the cylinder (Fig. 1c) is assumed. The length of the path from point **p** to point **q** on the upper boundary of the vegetation in direction **d** is specified by:

$$q_z(\lambda) = h_t \tag{26}$$

Substitution in eq. (21) results in the path length:

$$\lambda = \frac{h_t - p_z}{d_z} \tag{27}$$

Light distribution

Light intensity on top of the canopy derives directly from the way the light climate is defined. External (free sky) light climate is given by:

$$i_{fl}^{\Omega}(\vartheta_i) = i_{fl,0}^{\Omega}(1 - (\sin\vartheta_i)^c) \tag{28}$$

where i_{fl}^{Ω} is the free light intensity per steradian (µmol $m^{-2}s^{-1}sr^{-1}$) for direction $\mathbf{d}_i$, and $i_{fl,0}^{\Omega}$ is the light intensity per steradian coming from the zenith direction. The light intensity is a function of the polar angle of direction $\mathbf{d}_i$. This dependence on θ_i is given by the factor:

$$(1-(\sin\vartheta_i)^c)$$

in which c is an empirical parameter.

If c is sufficiently high, the light intensity i_{fl}^{Ω} will converge to the light intensity $i_{fl,0}^{\Omega}$ so that a uniform light intensity over the sky will be the result.

Light intensity per steradian $i_{fl,0}^{\Omega}$ from the zenith direction is related to the horizontal light intensity I_H (µmol $m^{-2}s^{-1}$) for the free sky by:

$$i_{fl,0}^{\Omega} = \frac{I_H}{2\pi\int_0^{\frac{\pi}{2}} \sin\vartheta_i \cos\vartheta_i (1-(\sin\vartheta_i)^c) d\vartheta_i} \tag{29}$$

For the analyses in this chapter empirical values I_H=1000 and c=2 are used.

Numerical integrations

All integrations described analytically above were implemented numerically in the form of Gauss-Legendre procedures (Press 1989). For the analyses in this chapter the number of quadrature points for each integration was set to 6.

List of symbols

a, b, c	Semi-axes of crown ellipsoid *E* (m)
a_L	Leaf light absorption coefficient
a_N	Scaling coefficient of nitrogen distribution
a_p, b_p, c_p	Coefficients of the P_{max}–*N* relation
a_R, b_R	Coefficients of the R_d–*N* relation
A_k	Area on a unit sphere (m^2) for direction class *k*
d_i, ψ_i, θ_i	Cartesian light direction vector and its two spherical components
d_L, ψ_L, θ_L	Leaf normal vector and its two spherical components
E	Surface function of the crown ellipsoid
f	Leaf area density (m^2m^{-3})
f'_k	Fraction of the total leaf area density for direction class *k*
f^{Ω}	Leaf area density per steradian (m^{-3})
i^{Ω}	Light intensity per steradian (µmol $m^{-2}s^{-1}sr^{-1}$)
i_{fl}^{Ω}	Free light intensity per steradian (µmol $m^{-2}s^{-1}sr^{-1}$)

$i_{fl,0}^{\Omega}$	Free light intensity per steradian (µmol $m^{-2}s^{-1}sr^{-1}$) from zenith direction
I_0	Photon flux density at the top of the crown (µmol $m^{-2}s^{-1}$)
I_n	Light absorption rate per unit volume (µmol $m^{-3}s^{-1}$)
I_L	Light absorption speed per unit leaf area (µmol $m^{-2}s^{-1}$)
K_E, K_V	Extinction coefficients for crown and vegetation respectively
N	Nitrogen content of leaves (mmol m^{-2})
N_0	Nitrogen content of a fully illuminated leaf (mmol m^{-2})
P_{max}	Maximum (light saturated) photosynthetic rate (µmol $m^{-2}s^{-1}$)
P_E	Net photosynthetic rate of the crown (µmol s^{-1})
P_L p_L	Net photosynthetic rate per unit leaf area (µmol $m^{-2}s^{-1}$)
P_n	Net photosynthetic rate per unit crown volume (µmol $m^{-3}s^{-1}$)
R_d	Dark respiration (µmol $m^{-2}s^{-1}$)
λ_E, λ_V	Path length through crown and vegetation respectively (m)
ϕ, θ	Quantum yield and curvature of the photosynthesis curve

Enrichment planting

Chapter 5

Improving species-site matching for enrichment planting: a model approach

submitted

Abstract

An often used method to accelerate and supplement forest regeneration is enrichment planting. Desirable species are planted in the natural vegetation or in the understory of plantations. When trees are planted in a natural vegetation stand, often lines are created from which the existing vegetation is removed. When trees are planted in a plantation the overstory vegetation is often thinned to increase light levels for the planted trees. The width of the line and the degree of overstory thinning affects growth and survival of target species differently depending on the characteristics of the surrounding vegetation and the target trees themselves, because species have different light requirements. Here a 3D-model approach was used to calculate light capture and photosynthetic rates of individual trees planted in different enrichment planting schemes in a secondary forest in Vietnam. The effects of varying line width, the degree of overstory thinning, planting trees in different successional stands of the same forest and planting trees in a forest stand with different light levels than the stand in which they were originally grown, were simulated. It was shown that the most suitable stand for species with different morphological and physiological traits (thus with different light requirements), the most appropiatel line width in a stand and the most appropiate degree of overstory thinning, can be predicted by mechanistically analysing ecological processes underlying tree growth. With this information species-site matching can be improved. This reduces the need for long-lasting and expensive experiments.

Introduction

In tropical regions the area of secondary forests is expanding due to the increased pressure on primary forests. However, natural forest regeneration after disturbance is often slow or stagnates (Aide et al. 1995; Chapman and Chapman 1999; Guariguata and Dupuy 1997; Hooper et al. 2004).

In recent years there has been increased attention for restoration ecology and in particular for management options to accelerate recovery of forests (Holl and Kapelle 1999; Parrotta et al. 1997). A widely applied management strategy for accelerated regeneration is enrichment planting. Desirable species are planted under a canopy of natural forest vegetation (d'Oliveira 2000; Ramos and del Amo 1992; Ricker et al. 1999) or in the understory of artificially created (timber) plantations (Lof et al. 2007; McNamara et al. 2006; Otsamo 2000) in order to increase the ecological and/or the economical value of the site.

A commonly used method of enrichment planting is line planting. In the existing forest, vegetation is removed (mostly understory and occasionally trees) in lines with a certain width in which the desired native species are planted (Bebber et al. 2002). The light levels created by the line depend on the width of the lines and the height and density of the surrounding vegetation (Ådjers et al. 1995; Montagnini et al. 1997; Pena-Claros et al. 2002). When desired species are planted under a (monospecific) plantation, sometimes the overstory vegetation is left intact and the understory, if present, is removed. Sometimes the overstory vegetation is thinned at the time of planting or in a later stage by pruning or selectively logging of neighboring trees to increase light levels for the underplanted tree species (McNamara et al. 2006; Otsamo 1998; Piotto et al. 2003).

Species have different light requirements (Dupuy and Chazdon 2006; Ramos and del Amo 1992), even closely related ones (Ådjers et al. 1995), while light requirements can also differ within a species with tree age (Davidson et al. 2002). Thus survival and growth of species are affected by the light levels at which they are planted. Studies that have shown variation in growth between underplanted tree species in response to different overstory densities, stress the importance of species and site selection and suggest further studies on species-site matching (Ådjers et al. 1995; Lof et al. 2007; McNamara et al. 2006; Montagnini et al. 1997; Otsamo 1998).

Ricker et al. (2000) studied growth of three tree species planted in mature primary forest, secondary forest and abandoned cattle pasture. They found that the three tree species differed in their light demands and suggested they should be planted in different forest types. Piotto (2007) performed a similar experiment with 24 species and suggested the same. Such experiments are valuable but require a lot of time, space and money (Korpelainen et al. 1995) and the outcome is usually restricted to a specific set of species in a specific vegetation type with possibly two, but rarely more, treatments (see Paquette et al. 2006).

In this study I apply the PHOLIAGE-model that is presented in chapter 4, in enrichment planting schemes in Vietnam. Native species were planted in two secondary forest plots differing in age, LAI, height and light conditions. In the younger plot vegetation was removed in lines in which the target species were planted while in the slightly older plot species were planted without the removal of overstory vegetation. The model calculates light capture and photosynthetic rate of individual trees in a vegetation stand. Tree and vegetation characteristics can be varied and the vegetation can be opened up to various extents. I have shown in chapter 4 that another method to accelerate succession, liberation of target trees, could be very well simulated with the model.

The validity of the model in enrichment planting schemes is tested by comparing the calculated photosynthetic rates of plants planted in the existing forest to observed growth data. I perform several simulations: (i) the effect of line width in the younger plot, (ii) overstory thinning in the older plot, (iii) planting species in different successional stands of the same forest and (iv) planting trees in a forest stand with different light levels than the stand in which they were originally grown.

Methods

Study area and species

The study sites are located in Bach Ma National Park, Thua Thien Hue Province, in central Vietnam (16°10’N 107°50’E). Bach Ma National Park was established in 1991 with a total area of 43,331 ha. It is the core of the last remaining contiguous forest belt in Vietnam, stretching from the South China Sea to the border with Laos. The area experiences high rainfall, especially from November until February (up to 8,000 mm per year). There is no distinct dry season and the vegetation, which consists mainly of secondary forest, is evergreen (Tran and Ziegler 2001).

In the park two plots were selected in which native species have been planted. One plot (hereafter referred to as plot 4) consists of young vegetation (mostly shrubs and lianas) of up to 4 m high in which lines of 2.5 m wide and 100 m in length have been created. Within each line vegetation was removed. Lines were located in East-West direction and were located approximately 5 m apart. Saplings of different species grown in nearby nurseries were planted in these lines in 2003, approximately 4-5 m apart. In the other plot (hereafter referred to as plot 8) the vegetation was left intact when native species were planted in 2001. The vegetation was 15 m high and consisted mainly of young trees. Some understory vegetation was present, especially in some parts where grasses were growing in tree fall gaps. Native species were planted in rows, approximately 4-5 m apart and with 5 m between the rows. The exact age and height of the saplings at the time of planting are unknown.

The studied species that were planted in both plots were: *Hopea odorata* (Dipterocarpaceae) and *Tarrietia javanica* (Sterculiaceae). In plot 4 also *Scaphium lychnophorum* (Sterculiaceae) and *Syzygium* sp. (Myrtaceae) were planted and in plot 8 *Sindora tonkinensis* (Fabaceae) and *Homalium hainanensis* (Flacourtiaceae) (hereafter species will be referred to by their generic names). All of these species are commonly used for their timber, except for *Scaphium* which is used for medicinal purposes.

Measurements

Individuals in plot 8 were selected and measured non-destructively in March 2005 and measured again in March 2006 to determine light capture, photosynthetic rate and above ground growth. The individuals in plot 4 were measured in March 2006 and October 2006.

Each time they were measured, height, leaf angle distribution, stem, branch and petiole dimensions (length and diameter), leaf dimensions (length and width of leaf blade), crown dimensions (length and width) and canopy openness were recorded for every individual. The percentage of canopy openness was determined with a densiometer. To calibrate the non-destructive measurements, individuals of the same species in the same height range as the saplings in the plots were collected from nurseries. Light availability in the nurseries was comparable to that in plot 4 but somewhat higher than in plot 8. The nursery plants were measured in the same way as the target plants and were subsequently harvested. All above-ground plant parts were dried (72 hours at 70°C) and weighed. Formulas describing the dry weight of the harvested plant parts were derived based on the plant dimensions that were measured non-destructively and plotted against the measured dry weight. The function that best described the measured dry weight (r^2 varied from 0.89 to 0.99) was used to estimate biomass of plant parts of the individuals in the plots from the non-destructive measurements.

Leaves (3-4) of each sapling in the plots were collected after the non-destructive measurements were finished. Fully exposed leaves from the top of the crown (i.e. leaves that were not shaded by other leaves on the same plant) were taken to determine maximum nitrogen content. A digital photograph of the leaves was taken to determine leaf area (SigmaScan Pro 5.0). All samples were dried in an oven for 72 hours at 70°C and weighed. Nitrogen content of the leaves was analysed with a continuous flow analyzer (SKALAR, Breda, the Netherlands) following the Kjeldahl method.

In March-June 2005, photosynthesis measurements were done in nurseries using an open gas exchange system (CIRAS 2, PP systems, Hitchin, UK) equipped with a LED light source. Leaves of varying age (young, medium and old: related to position on the branch) from different individuals (max. 3 leaves per individual, total 15-18 leaves per species) that were growing in nurseries were selected. Photosynthetic rates were measured early in the morning when stomata were open. Maximum photosynthetic rates were measured at Photosynthetic Active Radiation (PAR) values of 1200-1500 μmol $m^{-2}s^{-1}$. In order to determine dark respiration and quantum yield light was varied from 80 to 0 μmol $m^{-2}s^{-1}$ PAR in steps of 10-20 μmol $m^{-2}s^{-1}$. The CO_2 concentration in the chamber was kept at 370 ppm throughout all measurements.

Model calculations and simulations

The three-dimensional PHOLIAGE-model was used in this study. For a short description see '*Model description*' in chapter 4 and for a detailed description see Appendix I in chapter 4.

We assume a tree with specific crown dimensions placed in a vegetation stand with a specific canopy height (see Fig. 1, chapter 4). The length to width ratio of the ellipsoid crown can be varied such that vertically elongated, spherical and flatter broader crowns can be considered.

The canopy of the vegetation can be fully closed and thus surround and even overtop the tree, or it can be opened up as a gap around the tree. Characteristics of the tree and surrounding vegetation can be varied. With a technique called ray-tracing (Bartelink 2000; Pearcy and Yang 1996; Rohrig et al. 1999) the amount of light absorbed in each point in the tree's crown is calculated and subsequently the photosynthetic rate for each point is calculated. An integration over all points is made to calculate whole crown light capture and photosynthetic rate.

For each individual of all species in both plots, instantaneous whole crown light capture and photosynthetic rates were calculated at the beginning and the end of the period in which growth was determined (March 2005 and March 2006 for the individuals in plot 8 and March 2006 and October 2006 for the individuals in plot 4). Dividing light capture and photosynthetic rate by leaf area gives light capture per unit leaf area (Φ_{area}: μmol $m^{-2}s^{-1}$) and photosynthetic rate per unit leaf area (P_{area}: μmol $m^{-2}s^{-1}$) respectively. These relative parameters allow us to compare species and individuals with different height and leaf area.

Next, simulations were done. First, species that were planted in one of the plots were digitally planted in the plot in which they did not occur. Second, the effect of different line widths on the photosynthetic rate of saplings in plot 4 was simulated. Third, *Hopea* was digitally planted in different successional stands younger than plot 4 (with varying LAI and height) with different line widths. Fourth, the effect of overstory thinning (varying LAI) was simulated in plot 8.

Statistical analyses

Species-effects on mean values of Φ_{area}, P_{area} and above ground Relative Growth Rate (RGR) were done with ANOVA-tests with a Bonferroni (equal variances assumed) or Games-Howell (equal variances not assumed) post-hoc test. The slopes in the above ground growth-average photosynthetic rate relation were analysed with linear regression and ANCOVA-tests.

Results

Light capture and photosynthetic rate

Mean values of morphological and physiological characteristics of species planted in plots 4 and 8 and mean characteristics of the vegetation surrounding the planted species are given in Table 1 and 2.

Table 1 Mean plant and vegetation characteristics in enrichment planting plots in Vietnam

	Plant characteristics																			Vegetation characteristics						
Plot	Species	n	height		crown axes (diameter in m)						crown l:w	leaf area		lad	leaf angle distribution			N_0		LAI		line width	height	leaf angle distribution		
			(m)	se	x	se	y	se	z	se		(m^2)	se	(m^2 m^{-3})	15	45	75	(mmol m^{-2})	se	(m^2 m^{-2})	se	(m)	(m)	15	45	75
4	*Hopea*	50	0.94	0.06	0.39	0.04	0.33	0.03	0.44	0.04	1.22	0.158	0.04	5.34	0.48	0.40	0.12	102.73	3.67	2.26	0.22	2.5	4	0.24	0.43	0.33
	Tarrietia	66	0.73	0.02	0.38	0.01	0.36	0.01	0.42	0.02	1.13	0.189	0.00	6.30	0.44	0.40	0.16	82.94	3.37	1.86	0.16	2.5	4	0.24	0.43	0.33
	Scaphium	41	0.50	0.05	0.14	0.03	0.15	0.02	0.22	0.03	1.49	0.026	0.02	10.98	0.21	0.40	0.39	84.43	2.22	2.01	0.11	2.5	4	0.24	0.43	0.33
	Syzygium	21	0.58	0.05	0.22	0.02	0.19	0.02	0.34	0.04	1.69	0.068	0.01	9.35	0.67	0.30	0.04	76.49	3.82	2.17	0.25	2.5	4	0.24	0.43	0.33
8	*Hopea*	23	0.82	0.07	0.41	0.03	0.38	0.05	0.35	0.07	0.89	0.048	0.01	1.71	0.64	0.28	0.07	74.32	5.12	5.39	0.81	0	15	0.24	0.43	0.33
	Tarrietia	49	0.95	0.06	0.40	0.04	0.41	0.04	0.43	0.04	1.06	0.125	0.01	3.37	0.68	0.28	0.04	87.16	5.61	3.76	0.32	0	15	0.24	0.43	0.33
	Sindora	10	0.93	0.04	0.33	0.03	0.27	0.03	0.33	0.04	1.12	0.056	0.01	3.75	0.49	0.31	0.20	77.41	1.94	3.54	0.38	0	15	0.24	0.43	0.33
	Homalium	27	0.68	0.04	0.39	0.02	0.31	0.02	0.33	0.03	0.95	0.080	0.01	3.90	0.80	0.20	0.01	58.06	2.31	4.15	0.18	0	15	0.24	0.43	0.33

Note: n indicates the number of plants incorporated in this study, crown axes x and y are the horizontal axes, z is crown length, crown l:w is the length to width ratio, lad is leaf area density, leaf angle distribution is divided in three classes indicated by 15, 45 and 75 degrees, No is the nitrogen content of the leaves in the top of the crown, s.e. indicates standard error of the mean

Table 2 Photosynthetic characteristics of planted species: quantum yield, dark respiration, maximum photosynthetic rate (P_{max}) and photosynthetic nitrogen use efficiency (PNUE)

Species	quantum yield (μmol C PPFD^{-1})	dark respiration (μmol m^{-2}s^{-1})	P_{max} (μmol m^{-2}s^{-1})	PNUE (μmol C mmol N^{-1}s^{-1})
Hopea	0.031	0.12	5.90	0.093
Tarrietia	0.026	0.42	5.48	0.063
Scaphium	0.028	0.23	5.33	0.058
Syzygium	0.021	0.04	1.46	0.021
Sindora	0.030	0.75	5.95	0.086
Homalium	0.025	0.62	1.36	0.037

Model calculations of instantaneous light capture and photosynthetic rate and per unit leaf area are shown in Fig. 1. Whole crown light capture and photosynthetic rate were divided by leaf area in order to compare differences among species with a different height and leaf area. In plot 4 light capture per unit leaf area (Φ_{area}) was highest for *Hopea* and lowest for *Scaphium* and *Tarrietia* (Fig. 1a) (ANOVA, $p<0.001$). *Syzygium* did not differ from the other species (ANOVA, $p>0.05$). *Syzygium* had less leaf area than *Hopea* (Table 1) but due to its smaller crown, Φ_{area} was nearly as high as that of *Hopea*. *Scaphium* had the smallest leaf area but high leaf area density (resulting in relatively strong self-shading) causing it to have a relatively low value of Φ_{area}, while *Tarrietia* had the most leaf area.

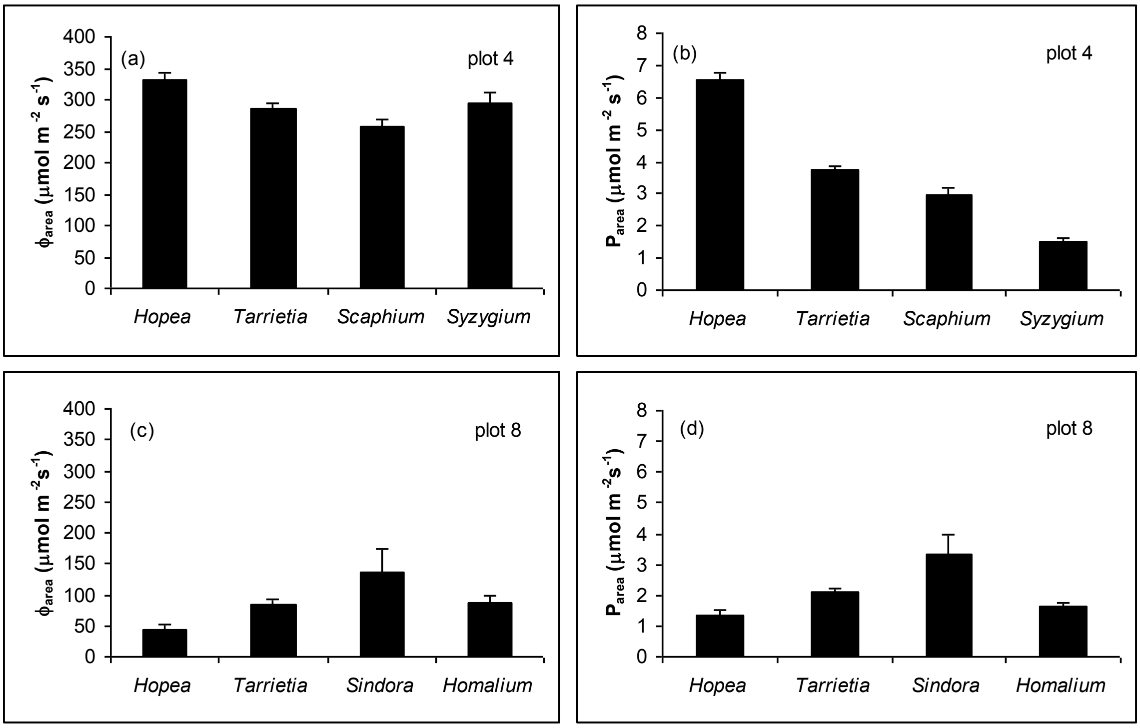

Fig. 1a-d Light capture per unit leaf area (ϕ_{area}) and photosynthetic rate per unit leaf area (P_{area}) of species planted in enrichment planting plots (plot 4 and 8) in Vietnam. Bars denote standard error.

Photosynthetic rate per unit leaf area (P_{area}) differed for all species in plot 4 (Fig. 1b) (ANOVA, $p<0.001$) with *Hopea* having the highest, *Tarrietia* and *Scaphium* intermediate and *Syzygium* the lowest values. These results corresponded with their respective photosynthetic characteristics (Table 2) which determine how efficient the captured light is used for photosynthesis. *Hopea* had a high leaf nitrogen content, high P_{max}, high photosynthetic nitrogen use efficiency (P_{max}/N_o) and a high quantum yield. Its dark respiration was relatively low. Its high Φ_{area} and favorable photosynthetic traits resulted in high P_{area}. *Syzygium* had a low leaf nitrogen content, low P_{max}, low nitrogen use efficiency, low quantum yield and low dark respiration. Even though it had a high Φ_{area}, due to its photosynthetic traits its P_{area} was low. *Tarrietia* and *Scaphium* had intermediate leaf nitrogen content, quantum yield and nitrogen use efficiency values, high P_{max} and high dark respiration and which resulted in intermediate P_{area} values.

Overall light levels in plot 8 were lower than in plot 4, resulting in lower Φ_{area} and P_{area} values. Φ_{area} was lowest for *Hopea* (Fig. 1c) (ANOVA, p=0.002). *Tarrietia, Sindora* and *Homalium* did not significantly differ from each other (ANOVA, p>0.05). *Hopea* had the lowest value because plants of *Hopea* were coincidentally planted at sites that were darker than the sites in which the other species were planted; the average LAI of its surrounding vegetation is higher for *Hopea* than for the other species (Table 1). This resulted in a low P_{area}. P_{area} tended to be highest for *Sindora* but differences between the species were not significant (Fig. 1d) (ANOVA, p>0.05). *Sindora* had a high P_{max}, nitrogen use efficiency and quantum yield (Table 2) which indicated an efficient use of the captured light and thus a high P_{area}. *Homalium* had low leaf nitrogen content, P_{max}, nitrogen use efficiency and quantum yield causing it to have a low P_{area} value similar to that of *Hopea,* despite its higher light capture than that of *Hopea*.

Overall, the species in plot 4 had more elongated crowns whereas the species in plot 8 had more spherical crowns. This trend was also observed for the two species planted in both plots: *Hopea* and *Tarrietia* (see l:w ratio in Table 1).

The above ground growth rate (g day^{-1}) within a 154-day period for individuals in plot 4 and a 360-day period for individuals in plot 8, was plotted against the average photosynthetic rate of the beginning and the end of that period (Fig. 2). All species showed strong positive correlations. In plot 4 the slope of the relation was highest for *Syzygium*, intermediate for *Tarrietia* and *Scaphium* and lowest for *Hopea* (ANCOVA, p<0.001). In plot 8 slopes were higher for *Hopea* and *Tarrietia* than for *Sindora* and *Homalium*. For *Hopea* the slope was higher and for *Tarrietia* it was lower in plot 8 than in plot 4.

Above ground Relative Growth Rate (RGR) (Fig. 3) in plot 4 was highest for *Hopea* and lowest for *Scaphium* and *Tarrietia* (ANOVA, p=0.001). *Syzygium* did not differ significantly differ from the other species (ANOVA, p>0.05). In plot 8 RGR was lowest, even negative, for *Homalium* (ANOVA, p=0.001). The other species did not differ significantly from each other (ANOVA, p>0.05). RGR was lower for *Hopea* and *Tarrietia* in plot 8 than in plot 4 (ANOVA, p<0.001 and 0.004 resp.).

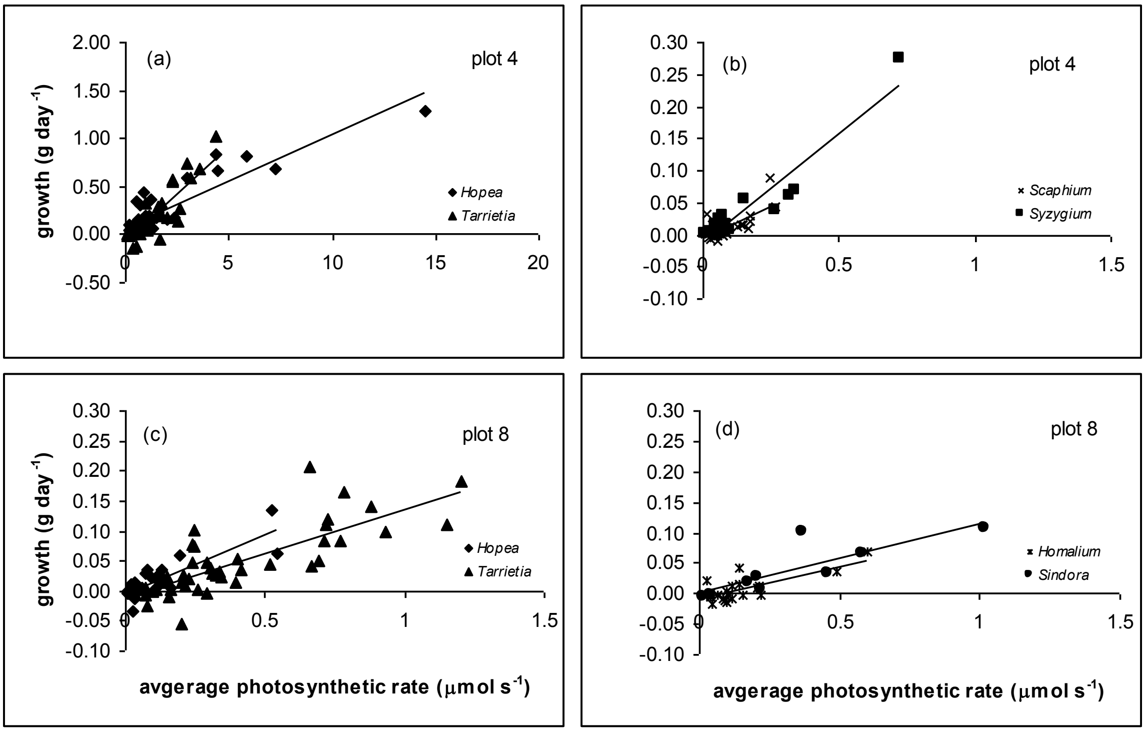

Fig. 2a-d Relation between observed growth and calculated photosynthetic rate (average of the beginning and the end of the period in which growth was observed) of species planted in enrichment planting plots (plot 4 and 8) in Vietnam. All relations are significant (linear regression, $p<0.05$) and r^2 values vary from 0.567 to 0.8975. For clarity two species per window are presented. Note the different scaling in window a.

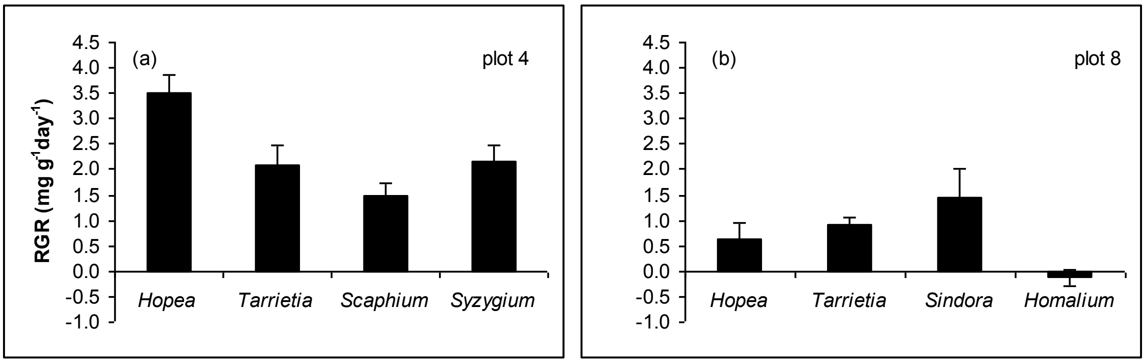

Fig. 3a-b Above ground Relative Growth Rate (RGR) of species planted in enrichment planting plots (plot 4 and 8) in Vietnam. Bars denote standard error.

Model simulation: crossplanting

The individuals of the two species that were planted in either one of the plots, *Sindora* and *Homalium* in plot 8 and *Scaphium* and *Syzygium* in plot 4, were digitally planted in the plot in which they did not occur. Average vegetation characteristics were used for the simulation: line width 2.5 m, height 4 m, LAI 2.04 for plot 4 and line width 0 m, height 15 m, LAI 4.18 for plot 8. *Scaphium* and *Syzygium* were calculated to have a lower carbon gain when planted in plot 8 (Fig. 1b & 4a) (ANOVA, $p<0.001$ for both species). They experienced a two-fold higher LAI from the surrounding vegetation in plot 8 than in plot 4, the vegetation was higher and they were not planted in a line. *Sindora* and *Homalium* had higher P_{area} values when planted in plot 4 (Fig. 1d & 4b) (ANOVA, $p=0.027$ for *Sindora* and $p<0.001$ for *Homalium*). *Sindora* and *Homalium* experienced a lower LAI when planted in plot 4, the vegetation height was lower and they were planted in a line.

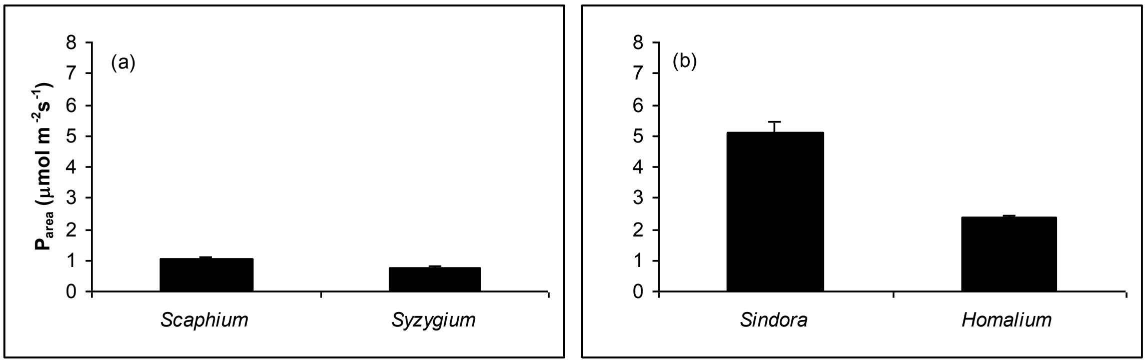

Fig. 4a-b Photosynthetic rate per unit leaf area (P_{area}) of species digitally planted in the plot in which they did not occur. Individuals of *Scaphium* and *Sygyzium* were planted in plot 8 and individuals of *Sindora* and *Homalium* were planted in plot 4. For mean species characteristics see Table 1.

Model simulation: variable line widths

All individuals of the species in plot 4 and 8 were grouped in three height classes: the 1/3 smallest, 1/3 intermediate and 1/3 tallest trees. Average values for sapling height, crown dimensions, leaf area, leaf angle distribution and leaf nitrogen content were calculated for each height class based on the individuals in that height class (Table 3). In general the taller saplings within a species had more leaf area and a greater crown volume. Leaf area density decreased with sapling height. Changes in line width were simulated in plot 4 for these average saplings. The average vegetation height was set to 4 m and the LAI was 2.04, as measured in the field.

Table 3 Mean values of species planted in enrichment planting plots in Vietnam when individuals are grouped into three height classes

Plot	Species	class	height	crown axes (diameter in m)			crown vol.	leaf area	lad	leaf angle distribution			N_0
			(m)	x	y	z	(m^3)	(m^2)	(m^2 m^{-3})	15	45	75	(mmol m^{-2})
4	*Hopea*	1	0.50	0.29	0.22	0.25	0.01	0.05	5.77	0.65	0.31	0.04	94.87
		2	0.87	0.32	0.32	0.38	0.02	0.10	5.00	0.47	0.42	0.11	108.04
		3	1.46	0.55	0.46	0.68	0.09	0.32	3.54	0.31	0.48	0.20	105.61
	Tarrietia	1	0.41	0.25	0.21	0.23	0.01	0.06	8.57	0.34	0.40	0.26	74.37
		2	0.64	0.33	0.36	0.34	0.02	0.13	6.15	0.50	0.40	0.10	76.31
		3	1.14	0.55	0.52	0.68	0.10	0.38	3.75	0.47	0.41	0.13	98.14
	Scaphium	1	0.37	0.08	0.10	0.14	0.00	0.02	26.52	0.15	0.46	0.39	85.37
		2	0.48	0.14	0.14	0.20	0.00	0.02	11.94	0.31	0.26	0.43	89.29
		3	0.65	0.21	0.21	0.31	0.01	0.04	5.43	0.18	0.47	0.35	78.25
	Syzygium	1	0.38	0.17	0.15	0.22	0.00	0.03	8.99	0.58	0.35	0.06	75.15
		2	0.54	0.22	0.16	0.25	0.00	0.05	9.97	0.74	0.24	0.02	67.47
		3	0.83	0.26	0.25	0.55	0.02	0.13	7.02	0.67	0.30	0.03	86.85
8	*Hopea*	1	0.50	0.31	0.24	0.22	0.01	0.03	3.86	0.70	0.26	0.04	67.00
		2	0.91	0.46	0.46	0.44	0.03	0.04	1.34	0.65	0.25	0.09	70.68
		3	1.08	0.45	0.44	0.40	0.04	0.07	1.71	0.57	0.35	0.08	86.85
	Tarrietia	1	0.70	0.31	0.31	0.33	0.02	0.08	4.81	0.72	0.25	0.02	84.44
		2	0.93	0.43	0.45	0.45	0.05	0.13	2.86	0.73	0.23	0.04	85.39
		3	1.24	0.47	0.48	0.52	0.06	0.17	2.76	0.59	0.35	0.06	91.81
	Sindora	1	0.75	0.28	0.26	0.23	0.00	0.04	12.36	0.46	0.33	0.22	69.96
		2	0.97	0.31	0.18	0.29	0.01	0.05	5.85	0.71	0.23	0.06	78.31
		3	1.14	0.41	0.36	0.52	0.04	0.08	2.11	0.30	0.38	0.32	86.46
	Homalium	1	0.48	0.33	0.29	0.21	0.01	0.05	5.25	0.86	0.14	0.01	51.05
		2	0.64	0.31	0.27	0.32	0.01	0.06	4.39	0.81	0.18	0.01	64.34
		3	0.93	0.52	0.36	0.47	0.05	0.13	2.72	0.72	0.27	0.01	58.79

Absolute instantaneous photosynthetic rates were plotted against line width (Fig. 5a-d). *Hopea* and *Tarrietia* had higher photosynthetic rates than *Scaphium* and *Syzygium*, largely because their leaf area was greater. For all species the tallest sapling reached the highest values and the smallest sapling the lowest. This corresponds to increase in leaf area with sapling height.

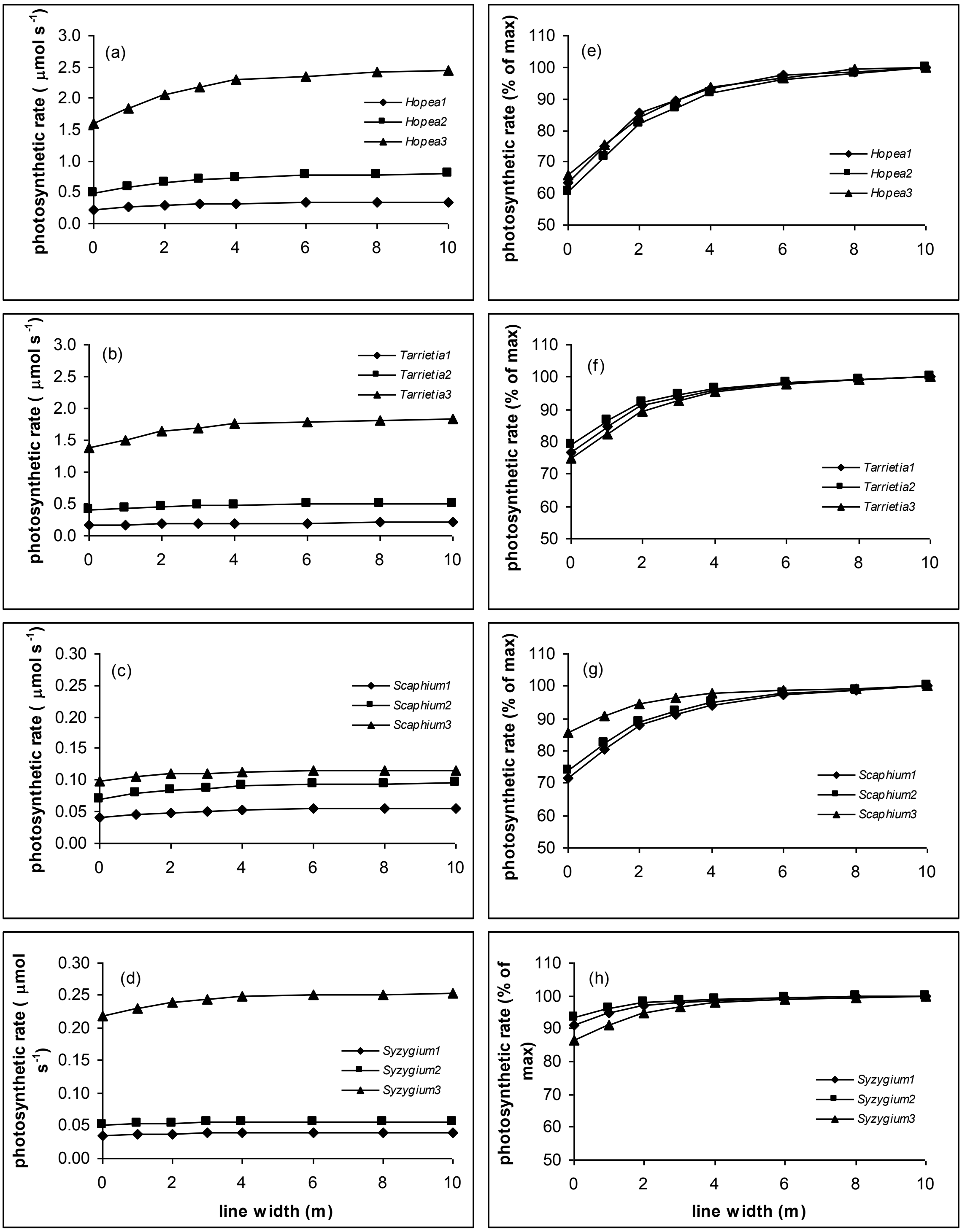

Fig. 5a-h Absolute instantaneous photosynthetic rate (a-d) and photosynthetic rate as percentage of the maximum (line width of 10 m) (e-h) plotted against the line width for saplings of different height in plot 4 (height 4 m; LAI 2.04). The number behind the species name denotes the corresponding height class: 1, small; 2, intermediate; 3, tall (Table 3). Note the different scaling in windows a-b and c-d.

Photosynthetic rate as a percentage of the maximum photosynthetic rate (at a line width of 10 m) was plotted against line width (Fig. 5e-h). When saplings were digitally planted in the intact vegetation (line width=0 m), *Syzygium* reached the highest, *Scaphium* and *Tarrietia* intermediate and *Hopea* lowest photosynthetic rate as percentage of the maximum. A larger line width was needed for *Hopea* to reach near-maximum photosynthetic rates than for the other species.

Hopea had the highest photosynthetic capacity thus this species needed more light to reach maximum values. The opposite was true for *Syzygium*. It had the lowest photosynthetic capacity and reached near-maximum levels of photosynthesis before the other species did. Small within species differences occurred but these were not directly related to sapling height.

In short, this analysis showed that line width differently affected the photosynthetic rate of species and of saplings of different height which implies different leaf areas.

Model simulation: Hopea planted in different successional stands

Of all species in plot 4 *Hopea* seemed the most sensitive to changing line width in the vegetation. Therefore the effect of line width in different successional vegetation stands on photosynthetic rate of the intermediate height class sapling of *Hopea* was simulated (Fig. 6). The successional stands varied in age which was expressed in height and LAI, with the younger stands having a lower height and LAI than the older stands. Leaf area density in all stands remained equal to that of the vegetation stand as in the field (vegh4 indicated the vegetation height and LAI as measured in the field). A lower vegetation height resulted in increased photosynthetic rates for *Hopea*. The lower the vegetation height, thus the younger the stand, the smaller the line width needed to be for *Hopea* to reach near-maximum photosynthetic rates.

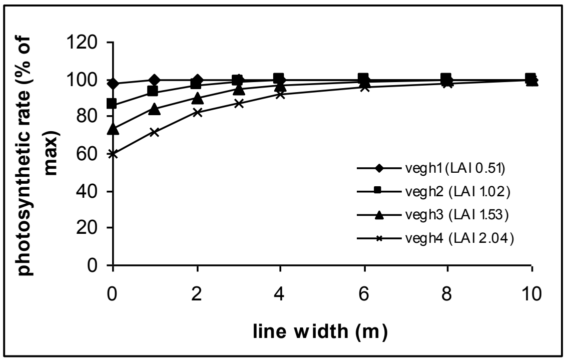

Fig. 6 Photosynthetic rate as percentage of the maximum (at a line width of 10 m) plotted against the line width for *Hopea*2 (intermediate height class, see Table 3) for four different vegetation heights (vegh; number denotes height in m) (leaf area adensity was kept constant). Vegh4 indicates the stand as measured in the field (height 4 m, LAI 2.04).

Model simulation: overstory thinning

Overstory thinning is done to increase light levels for underplanted trees by decreasing the LAI of the surrounding vegetation. The effect of LAI on photosynthetic rate was simulated for the average saplings in plot 8. The vegetation height remained 15 m throughout the simulation, as measured in the field. Absolute instantaneous photosynthetic rates were plotted against LAI values (Fig. 7a-d). For all species the tallest sapling achieved highest and the smallest sapling lowest photosynthetic rates. This related to the increase in leaf area with sapling height. Photosynthetic rate as a fraction of the photosynthetic rate at a LAI of 4.18 (measured in the field: set to 1) was plotted against the LAI of the vegetation (Fig. 7e-h). For all species a LAI higher than 4.18 resulted in lower photosynthetic rates and a lower LAI had an opposite effect. The effect of overstory thinning was less for *Homalium* than for the other species. It had a low photosynthetic capacity and a low quantum yield. Apparently it had reached relatively high rates of photosynthesis at a LAI of 4.18 so a decrease in LAI did not increase its photosynthetic rate as much as for the other species. Small within species differences occurred between saplings of different height.

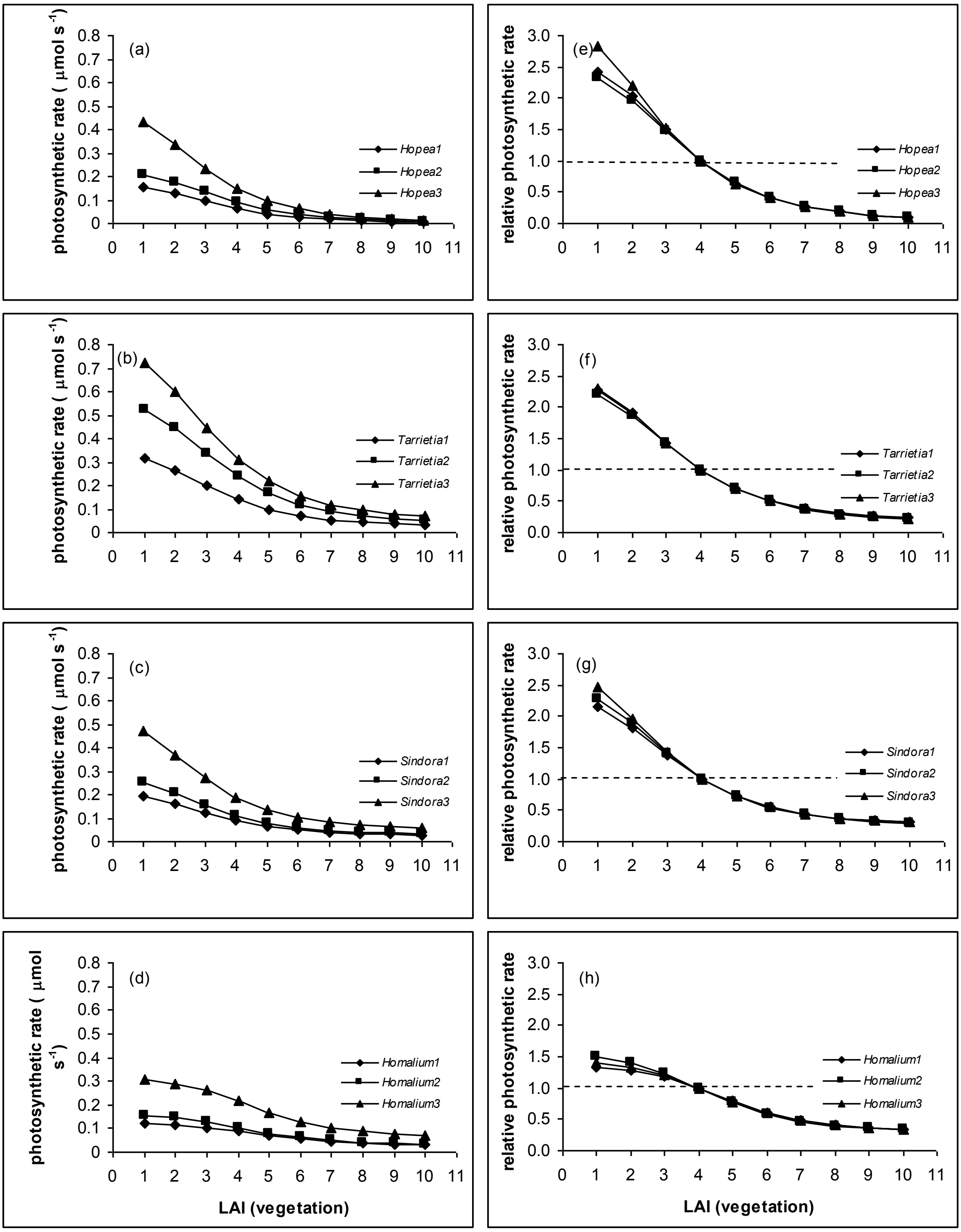

Fig. 7a-h Absolute instantaneous photosynthetic rate (a-d) and relative photosynthetic rate as compared to the value at a LAI of 4.18 (as measured in the field; set to 1) (e-h) for saplings of different height in plot 8 (line width 0 m, height 15 m). The number behind the species name denotes the corresponding height class: 1, small; 2, intermediate; 3, tall (Table 3). The dashed line shows the photosynthetic rate in the field.

Discussion

The measurements and model calculations have shown that species used for enrichment planting in Bach Ma NP have different light requirements. Height, LAI and line width of the existing vegetation determine the light levels planted saplings receive and these saplings in turn respond differently depending on their morphology and physiology. With the model approach presented here the effects of changes in the existing vegetation (i.e. line width, overstory thinning) on photosynthetic rates of planted saplings can be simulated. With this information species-site matching in enrichment planting schemes can be improved with a much smaller reliance on long-lasting and expensive experiments because the model, using a mechanistic analysis of the fundamental ecological processes underlying growth of planted trees, makes it possible to calculate the immediate and ultimate effects of commonly used field practices.

Even though the gaps surrounding target individuals in the model are circular, I argue that the model is also suitable to calculate photosynthetic rates of individuals trees planted in lines. An increase in line width is qualitatively comparable to the increase in radius of a circle as both entail an increase in the distance between a target plant and the surrounding vegetation. Quantitatively, light capture and photosynthetic rates of trees grown in a line might differ from those grown in a gap since more light reaches the tree in a line with a width similar to a gap with that diameter, because a line is longer in the other direction. Furthermore light availability in a line seems to depend on its direction, with respect to the position of the sun (Ådjers et al. 1995).

Light capture, photosynthetic rates and observed growth differed between species and plots. Between species differences could be related to their morphological (height, leaf area, crown volume) and physiological traits (leaf nitrogen content, maximum photosynthetic rates, nitrogen use efficiency, quantum yield, dark respiration). Between plot differences in turn were largely related to the concomitant differences in light availability. Greater light capture and photosynthetic rates were calculated for species in the younger plot 4 with lower surrounding vegetation and a better light climate for the planted seedlings. This corresponded with higher growth rates in this plot as compared to the older, darker plot 8.

When the species that occurred in plot 4 were planted in plot 8, they experienced a higher LAI of the surrounding vegetation and a more than three-fold higher height of that vegetation. Consequently light capture and net photosynthetic rates decreased considerably. Since *Scaphium* had photosynthetic traits comparable to that of a relatively light demanding species, high photosynthetic capacity and high dark respiration (Reich et al. 1994), it is no surprise that planting this species in plot 8 resulted in considerably lower values for P_{area}. It decreased with 64%. *Syzygium* however, had photosynthetic traits comparable to that of shade-tolerant species: low photosynthetic capacity and low dark respiration, which makes it suitable for darker environments. Light levels in plot 8 apparently were too low for this species because the P_{area} value decreased with 49%. The decrease is less than for *Scaphium* because of its shade-tolerant character. *Sindora* had photosynthetic traits that were similar to those of a relatively light demanding species: high photosynthetic capacity and a high dark respiration. When it was planted in a lighter plot than the plot in which it originally occurred, the P_{area} value increased with 55%. The same holds for *Homalium* but since it is a shade-tolerant species, the increase was somewhat lower (48%).

If trees are grown in nurseries with light levels that differ largely from the forest in which these trees are going to be planted, than this could affect the initial performance of trees once they are planted in the forest. Also when management practices are applied that result in large changes in light levels, trees may not be able to plastically adapt to the new light levels because there is a limit to which plants are able to adapt to the prevailing light levels. The degree to which plants are able to acclimate differs per species, depending on their level of shade tolerance and their maximum growth potential (Chazdon 1992). This restriction in acclimation should be considered when selecting species and nursery conditions, when planting trees and when opening up the vegetation.

It might be that since the time of planting, the individuals of the planted species acclimated to the light conditions they are growing in (Kitajima 1994). It has been hypothesized that trees growing at lower light levels should have broad crowns with few leaf layers in order to reduce self-shading, whereas trees in high light environments should have elongated crowns with numerous leaf layers (King 1990) to maximise light capture. The opposite is often found in the field however (Kitajima et al. 2005; Poorter and Werger 1999; Selaya et al. 2007; Sterck et al. 2001). In our study species growing in the darker plot 8 tended to have less elongated crowns, as indicated by the length to width ratio, than the species in the lighter plot 4. This also holds for the two species that were planted in both plots. This indicates that at least in these latter two species acclimation at the level of crown structure to existing light levels occurred. This implies that planting of certain species in environments with great differences in light as compared to the environment where they grew in before planting, may not necessarily increase photosynthetic rates immediately as they need time to adjust to the new light levels.

All species showed positive correlations between growth and the average of the photosynthetic rate calculated at the beginning and the end of the period in which growth was measured. When photosynthetic rate at the beginning of the period was plotted against growth, also significant positive correlations existed ($p<0.05$) (not shown) but r^2 values were lower. Growth was measured over relatively long periods, half a year for plot 4 and one year for plot 8, and in different periods. That implies that weather events might have affected the growth conditions of the species for some periods of time within the interval of measurements.

These sites were not stable in terms of environmental conditions. Several times a year typhoons and storms hit the area which severely damaged the forest. Larger trees lost leaves, branches or fell while shorter trees were damaged by the wind and also by falling branches or trees. The light climate in the forest was especially disturbed after a strong typhoon in November 2005 (Kai Tak) hit the area. This typhoon occurred within the period that growth was monitored in plot 8. This typhoon, and smaller typhoons and storms, may have caused differences in slopes of the growth-average photosynthetic rate relation that were found between species and plots. In such an unstable system it is probably more accurate to calculate growth over shorter periods.

Another reason for the different slopes that were found might be that species differed in measured dark respiration. A low dark respiration is often linked to low respiration values of non-photosynthesising plant parts. The low dark respiration of *Syzygium* could thus relate to low respiration values of the whole plant and this could contribute to its high slope. Nevertheless, the average values of the beginning and the end of the growth period correlated well with the observed growth, indicating that our model was accurate enough to predict growth of species planted in enrichment planting schemes.

Within a species, saplings of different height had different leaf areas and crown volumes and responded differently to a change in line width. I have shown that the line width at which maximum net carbon gain is achieved depends on the surrounding vegetation height and LAI and the saplings characteristics (height, leaf area, physiology) (see also chapter 4; Ådjers et al. 1995; Montagnini et al. 1997; Peña-Claros 2003; Ricker et al. 2000). Thus the optimal line width (line width at which a species reaches maximum carbon gain) will be different for species and even for saplings within a species if they greatly differ in height, and for forest stands of different successional status.

Ricker et al. (2000) and Piotto (2007) experimentally studied species performance in open pasture, secondary and mature forest and found species to perform differently in these contrasting environments. With our model I was able to make accurate estimates of photosynthetic rates of species planted in contrasting environments which reduces the need for such extensive planting experiments or experiments in which photosynthetic traits are measured on species grown at different light levels (Davidson et al. 2002). I have shown with a model approach that a species with a high photosynthetic capacity should better be planted in a young successional stand. This way, smaller line widths are needed for this species to reach near-maximum values of photosynthesis. Also when overstory thinning is applied species and sapling characteristics (i.e. leaf area, physiological traits) should be taken into account (see also Ricker et al. 2000). In this study the species that seemed more shade-tolerant were near to their maximum values of photosynthesis in the plots where they grew and little labor would have been needed to create sufficient light levels so that maximum photosynthesis levels were reached. This is favorable, particularly when the goal of the enrichment planting is to increase the economical value by planting timber species (often shade-tolerant) (De Graaf et al. 1999; Guariguata 1999; Piotto et al. 2003). Opening up the forest to such an extent that all target species will reach maximum growth will destroy the existing forest and it will require a lot of labor and thus money, while opening up the vegetation to smaller degrees will also considerable increase plant growth. If the costs of opening up the vegetation are known, our model can be used to calculate the optimal management regime in terms of increased plant growth and associated costs.

Here six species were used in the simulations, so one should take into consideration that when planting many different species within a plot, different light levels are needed. Lines of different width or patches with different overstory thinning treatments could be created in order to match the specific demand of the species planted. As noted, line cutting or overstory thinning may require a lot of labor (Korpelainen et al. 1995) especially when the forest is tall, dense or difficult to reach or when the area designated for enrichment planting is large. Less labor should be needed when saplings with sufficient leaf area or with the matching light requirements are planted (see also Ramos and del Amo 1992).

I have shown that with the model presented in chapter 4 accurate estimations of light capture and photosynthetic rates of trees planted in enrichment planting schemes can be made and that it is useful in planning enrichment planting activities. The optimal stand for species with different physiological traits, the optimal line width in a stand and the optimal level of overstory thinning can be predicted. The model thus provides a useful tool to mechanistically analyse growth of trees used in enrichment planting and saves considerably on labor for extensive experiments.

Measuring plants (0.5 year old stand)

Chapter 6

General discussion and summary

The area of secondary forests is expanding rapidly in tropical regions. After destruction of the primary forest or after abandonment of agricultural fields, secondary forest regeneration starts. First shrubs, grasses and herbaceous climbers that are able to recruit on degraded lands will dominate the area, after which pioneer trees take over. Later successional climax species grow in the understory and will dominate the forest after the pioneers die off (cf. Finegan 1984; Peña-Claros 2003). Unfortunately many regenerating forests never reach the climax stage. When shrubs, grasses or herbaceous climbers grow excessively in the first stage, growth of the pioneer trees is strongly inhibited because of the intense competition with the first stage plants. The process of succession is severely hampered in this way (Aide et al. 1995; Nykvist 1996; Woods 1989).

Since primary forests are rapidly disappearing (Hirsch 1997) secondary forests are becoming more important. Increasingly more people, especially those that are poor, depend on the resources and functions offered by secondary forests and therefore it is important to understand the successional process. Recently there has been a lot of attention for management options to accelerate the regeneration of tropical secondary forests (Holl and Kapelle 1999).

In this study fundamental research and applied research in tropical secondary forest succession were combined. The fundamental part of this study focused on natural regeneration of a forest. Individual plants of different species were followed in time during the very early stages of succession and the competition for light (chapter 2) and nitrogen-use efficiency (chapter 3) were related to the observed size hierarchy among plants. The applied part of this thesis focused on two management methods commonly used in forest restoration: liberation (chapter 4) and enrichment planting (chapter 5).

The role of asymmetric light competition and nitrogen-use efficiency

During forest succession the vegetation increases in height. Taller plants are able to deploy their leaves in the most illuminated layers of the canopy and therefore can capture more light than smaller plants (Givnish 1982). It is generally believed that taller plants capture more light relative to their size than smaller plants (Ford 1975; Schwinning and Weiner 1998). This asymmetric light capture is assumed to largely determine the course of succession by increasing size inequalities between plants (Huston and Smith 1987; Van Breugel 2007). Taller plants will become increasingly taller due to asymmetric light capture and as a result grow relatively faster, thereby outcompeting the smaller plants and this changes species composition. However, only few studies have measured the degree of asymmetry in light competition (Aan et al. 2006; Anten and

Hirose 1998; 1999; Hirose and Werger 1995; Werger et al. 2002) and only one has done this for a tropical secondary forest (Selaya et al. 2007).

Light capture alone does not determine the size hierarchy among plants. The efficiency by which light is used for photosynthesis also determines growth (Hikosaka et al. 1999; Schwinning 1996). Light use efficiency (LUE) is determined by a plant's physiological traits, such as maximum photosynthetic rate, quantum yield and respiration. The current dissertation is the first that related size dependent light capture and LUE to plant growth over time on the same plants in a secondary forest.

In chapter 2 I studied light competition among one woody shrub and three tree species, and related this to the observed size hierarchy that occurred during the first 5 years of succession. It appeared that all species had approximately similar values for light capture per unit above ground mass (Φ_{mass}) and LUE despite differences in average species height. In general, taller species captured slightly more light per unit leaf area (Φ_{area}) but due to small differences in the amount of leaf area per unit mass (leaf area ratio: LAR), Φ_{mass} was almost similar for taller and smaller species and within species for taller and smaller individuals (note that Φ_{mass}=Φ_{area}*LAR). This is in contrast to the general belief that asymmetric light capture, with taller plants capturing disproportionally more light, largely determines secondary succession. It is consistent with other studies that found similarity in Φ_{mass} between species of different size (Anten and Hirose 1999; Hirose and Werger 1995; Selaya et al. 2007). Hirose and Werger (1995) suggested that a similar Φ_{mass} facilitates species co-existence in a stand.

As a result of the absence of asymmetric growth, the size hierarchy that was observed six months after the plants had emerged, remained stable during at least the subsequent five years of succession. The vegetation stand became taller and denser but this did not increase the level of size-asymmetric growth or change the associated size hierarchy and thus species composition of the secondary forest remained the same. My study does not however preclude that asymmetric light competition may become more apparent in later stages of succession. At some point the smaller plants, for instance the shrub *Melastoma candidum*, will be overgrown by the taller plants. The smaller plants will be inhibited to grow tall either by architectural constraints or maybe due to stronger asymmetric light competition and will be outcompeted. The darker conditions created by the pioneer species will provide a suitable habitat for shade-tolerant species to grow. This will change species composition.

Besides light capture and light use efficiency also nitrogen-use efficiency may affect the size hierarchy among plants during forest succession (Aerts and Van der Peijl 1993). Nitrogen is an essential component of photosynthetic proteins (Evans 1989) and as a result of its limited availability it is one of the primary factors that limits plant growth (Kachi and Hirose 1983; Vermeer and Berendse 1983). Thus an efficient use of nitrogen for biomass gain may partly determine a plant's success during forest regeneration (Ellsworth and Reich 1996; Herbert et al. 2004; van der Werf et al. 1993).

Nitrogen-use efficiency is a function of a suit of traits including leaf life span, nitrogen resorption, leaf-level potential photosynthetic nitrogen-use efficiency but also plant height, crown structure, leaf area and nitrogen distribution. However, very little work has been done to quantitatively link these traits to nitrogen-use efficiency. I have build upon a concept developed by Hiremath (2000) to study the different components that determine whole canopy cumulative canopy nitrogen-use efficiency ($PNUE_{cum}$) in a detailed and integrated manner, taking traits such as plant height (i.e. canopy position), whole canopy light capture and nitrogen distribution in the canopy into account.

In chapter 3, $PNUE_{cum}$ and its underlying traits were determined for four species in two forest stands differing in age, height and LAI (also used in chapter 2). $PNUE_{cum}$ differed two-fold among species but these differences did not relate to the species position in the size hierarchy in this study. $PNUE_{cum}$ is the product of photosynthetic nitrogen productivity (PNP) and mean residence time of nitrogen (MRT). PNP did not differ among species in a stand. Differences in height between the species were relatively small and thus differences in light levels were also relatively small (see Φ_{area} values in chapter 2). The components determining MRT, leaf life span and nitrogen resorption, on the other hand varied greatly among species and consequently caused the differences in $PNUE_{cum}$.

A high MRT is likely to be advantageous in nutrient limited environments, where nutrient conservation rather than rapid growth is the key to persistence (Hiremath 2000). It was found previously that on soils with low fertility, species with high MRT instead of high PNP are favored (Aerts and de Caluwe 1994; Vazquez de Aldana and Berendse 1997; Yuan et al. 2005) though this was never before tested in tropical secondary forests. Our study site was very degraded due to effects of war followed by several slash and burn cycles of 5-6 years with very short fallow lengths (several months) thus a high nutrient retention and an efficient use of resources seems beneficial here (see also dos Santos et al. 2006).

In general, when plants grow taller they can reach the more illuminated layers of the canopy and thus increase light capture. This leads to a higher Φ_{area} and PNP. This height growth is facilitated by a rapid leaf production at the top of plants enabling such plants to shade competitors and thus achieve greater photosynthesis, growth and reproduction (Boonman et al. 2006). However placing leaves in the upper layers of the crown results in the abscission of leaves lower in the crown because resources, among which nitrogen, are reallocated in order to sustain rapid growth (Ackerly and Bazzaz 1995). This increases leaf turn-over and thus decreases leaf life span. A lower leaf life span decreases the MRT of nitrogen and consequently nitrogen-use efficiency decreases. This implies that if light capture, and consequently PNP, does not benefit the plant to the degree to which MRT decreases, nitrogen-use efficiency of a plant will decrease as it grows taller. This might affect a plant's performance, especially as nitrogen availability changes during succession (Ewel et al. 1991). Such trends were not observed in the current study. Vegetation development was relatively slow. This probably enabled species to physiologically acclimate to the changing light levels. Also, due to the open structure of the vegetation, light capture, and consequently PNP, did not increase with species height.

It was found previously that a plant cannot maximise nitrogen and light use efficiency simultaneously (Hirose and Bazzaz 1998). However, I found that the species with the highest (instantaneous) LUE also had the highest $PNUE_{cum}$. This species was the smallest of the four species studied thus a high nitrogen and light use efficiency did not relate to a tall stature.

Considering the results of chapter 2 and 3 it is likely that the initial seedling height determines the height of the saplings of pioneer species during subsequent succession (Boot 1996). Initial seedling height is determined by seed size, by an efficient use of seed resources for biomass allocation (height) in the seedling phase, or by small differences in timing of germination.

Forest restoration ecology

In chapter 2 and 3 I analysed processes underlying natural forest regeneration. As mentioned before, natural forest regeneration is often slow or stagnates, because shrubs, lianas or grasses invade degraded sites and they may compete with trees for resources (Berkowitz et al. 1995; Holl 1998; Parrotta et al. 2002; Putz and Canham 1992) or catch fire in the dry season that destroys young forest growth (Werger 1983). This strongly hampers forest succession.

Two commonly used methods to accelerate succession are liberation and enrichment planting. I used a model approach (PHOLIAGE) to analyse the results of a liberation experiment in a 1.5 year old secondary forest stand (chapter 4). The same approach was used to analyse growth of native species planted in two young forest stands as part of the many enrichment planting activities undertaken by Bach Ma NP within the framework of a large reforestation program launched by the Vietnamese government (chapter 5). Fundamental ecological processes that underlie tree growth were analysed in a quantitative manner to approach practical problems that occur during acceleration of succession.

When tree growth is hampered by strong competition with neighbors, liberation is potentially a useful management option to enhance tree growth (Collet et al. 1998; Finegan et al. 1999) and thus to accelerate succession. Liberation of target pioneer tree species in a 1.5 year old forest stand resulted in increased light capture and photosynthetic rates. Growth was increased with 34-49% depending on the species. The responses of species differed and were related to their height (relative to the vegetation height), leaf area, crown dimensions and their physiological traits, such as maximum photosynthetic rate and dark respiration.

The gap radius from which vegetation should be removed to maximize a species' photosynthetic rate depends on the light requirements of the target species, but, as I showed, also on the height and density of the surrounding vegetation which changes during succession. In early stages, when the vegetation stand was 0.5 years old and the vegetation height and density were relatively low, photosynthetic rates of pioneer trees were increased to 164-207% when vegetation was removed in a radius of 0.5 m. In a later stage (1.5 year old stand), when pioneer trees were closer to the top of surrounding vegetation canopy, vegetation removal resulted in a smaller increase in photosynthetic rate. It is therefore important to liberate trees early in succession so that the greatest effect is reached with the least amount of labor. With the

PHOLIAGE-model it can be studied what the effect is of liberation for each tree in a certain forest stand and the best liberation technique can be chosen.

When trees are no longer hampered in growth by the surrounding vegetation, their biomass allocation pattern seems to change. Less biomass is invested in height because the need to grow tall is reduced and instead trees create denser canopies (Collet et al. 1998). This is important in younger successional stands since shrubs, even though they are architecturally constrained to grow tall, can still keep up with tree height and thus overtop trees in such young stands. A denser tree crown will increase the shading out of the shrubs and grasses growing underneath the tree's crown. Once the tree has overtopped and (partly) shaded out the surrounding vegetation, it will be hampered considerably less in growth.

With the model approach I was also able to relate photosynthetic rates of native species planted in two existing forest stands differing in age, height and LAI, to their observed growth rates. Between species differences in photosynthetic rates could be related to their morphological traits, that affect light capture (height, leaf area, crown dimensions), and physiological traits, that relate to their light requirements (level of shade-tolerance). Between stand differences were related to the concomitant differences in light availability.

The more shade-tolerant species had photosynthetic rates that were near the values that they can potentially reach in the plots in which they grew. Digitally opening up the vegetation resulted in higher photosynthetic rates. The more light demanding species benefited more form opening up the vegetation since they needed more light to reach maximum values. Opening up the vegetation increased their photosynthetic rate by up to 40%. However, the vegetation would have to be opened up to a large extent which is practically not desirable or not realistic. For instance, by creating line widths of 5 m *Hopea odorata* would nearly reach its maximum photosynthetic rate. But creating lines of 5 m would cost a lot of labor, and thus money, and it would severely destroy the forest. Besides, by increasing light levels to such an extent, grasses and other undesirable species may start to grow and compete with the trees (McNamara et al. 2006). A smaller line width (2 m) would cause less damage to the forest and still it would increase photosynthetic rates of *Hopea odorata* by 30%. With the model calculations and simulations the most appropiate management option can be chosen, with taking tree growth and the amount of labor into account.

Many field experiments on liberation and enrichment planting have been done but they require a lot of time, space and money and results are restricted to a particular situation and generally cover limited amounts of experimental conditions and replication (Paquette et al. 2006). In chapters 4 and 5 I showed that the predicted photosynthetic traits of target trees based on model calculations, correlated well with the observed growth. This indicates that the model that I used was well able to predict growth of trees in early successional forests, whether they were naturally occurring or planted. Commonly used practices such as liberation, line planting and overstory thinning, could be well simulated so that recommendations about when and how to apply these practices can be made. In this way management activities can be done with a higher efficiency and with a reduced need for long-lasting and expensive experiments.

Potential applications of the model approach

In this study the PHOLIAGE-model was applied in an experiment in which pioneer trees were liberated and in two natural forest stands in which native species were planted. I argue that this model can also be applied in other situations where liberation is needed, for instance in an older, more developed forest in which the growth of later successional species needs to be stimulated to enhance succession. It could also be applied in liberation or planting schemes that have an economic incentive (De Graaf et al. 1999; Guariguata 1999). The effects of various management regimes on timber production, and thus on profits, can be calculated.

Another example in which this model approach might be very useful is in enrichment planting under plantations. Often in South East Asia degraded lands are invaded by undesirable plants, such as the grass *Imperata cylindrica* (McNamara et al. 2006; Otsamo et al. 1997). Fast growing exotic species are planted to prevent soil erosion and to quickly create a canopy cover to eliminate the grass. When a canopy has been created and the grass has been eliminated, native species are planted under the canopy of the exotic species to enrich the site (McNamara et al. 2006; Otsamo 2000). Often the canopy is thinned at the time of native species planting or in a later stage, to increase light levels for the underplanted species (McNamara et al. 2006; Otsamo 1998). But the effect of this thinning on subsequent growth of planted trees is usually not known and this management is therefore often carried by trial-and-error which is obviously costly and time-consuming.

A good example of where this methodology has been applied is in central Vietnam in the Hai Van area south of Phu Loc (McNamara et al. 2006). Many previously forested areas were converted into fire-prone grasslands (*I. cylindrica*) after the second Indochina war and did not recover. In 1986 trees of the exotic species *Acacia auriculiformis* were planted in different densities and they shaded out the grass several years after planting. The overstory canopy was thinned between 1993 and 2000 when native species were planted. The initial thinning appeared too much because grasses regrew and started competing with the native species. Later, the degree of thinning was reduced.

Various light levels throughout the planting site existed due to different *Acacia* planting densities and different levels of overstory thinning. Initially many different native species (approximately 40) were planted under the *Acacia* canopy but most of the planted species died, and later plantings focused on the relatively few surviving species (approximately 13). Apparently species and site did not match very well. The model presented in this dissertation can contribute to the success of species planting under plantations, by analysing the effect of various management practices and the resulting light levels, on the photosynthetic rate of the planted trees.

Using the PHOLIAGE-model

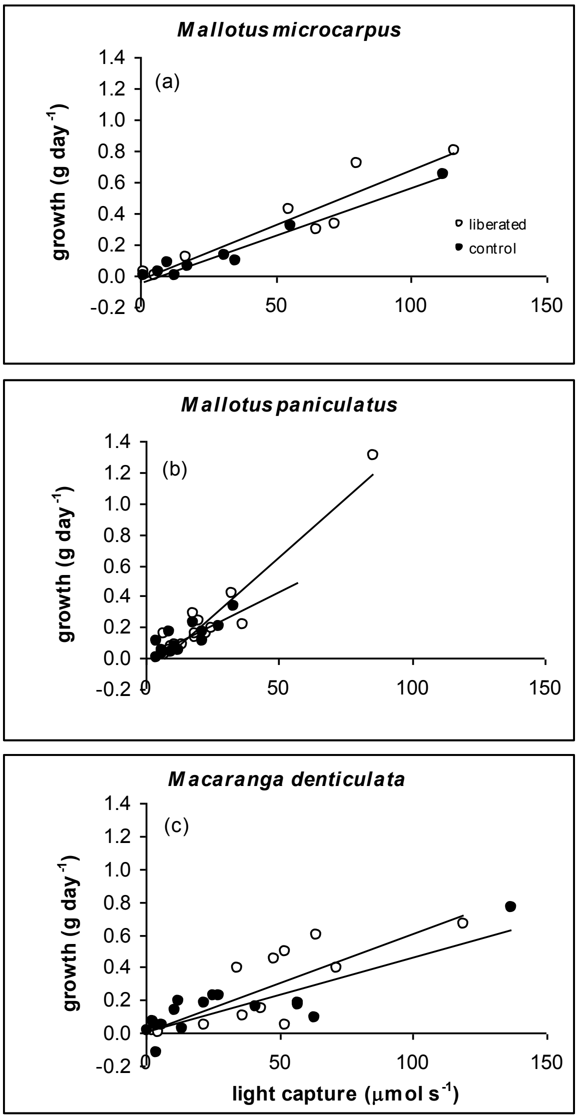

Fig. 1a-c Correlation between observed above ground biomass growth in 174 days after vegetation removal and calculated light capture immediately after vegetation removal. All correlations are significant (MM, $p<0.05$) and r^2 values varied from 0.6498 to 0.9635.

The PHOLIAGE-model is not the only 3D-model that calculates tree photosynthetic rates and is therefore not very innovative, but it is unique in that it is used to approach practical problems that occur in restoration ecology. The data needed to predict plant growth can be relatively easily and quickly gathered, in contrast to the data needed for some other, more detailed, tree growth models (Pearcy and Yang 1996; Sterck and Schieving 2007). Data to calculate light capture were gathered with a densiometer in this study and this has proven to be sufficiently accurate (chapter 4 and 5). Gathering few data is beneficial in liberation or enrichment planting activities since many trees and large areas of forest are concerned. The biggest obstacle will be the photo-synthesis measurements for which an expensive photosynthesis meter is needed. In tropical countries money and knowledge might be lacking to measure a plant's photosynthetic traits. But whole crown light capture strongly correlates with observed growth as well (Fig. 1 & 2) so in case photosynthesis measurements cannot be done, light capture data will most probably be sufficient. Data of the target trees and the surrounding vegetation are compiled into an excel spreadsheet which is 'read' by the model. The output is instantaneous whole crown light capture and photosynthetic rate for each individual tree.

In this study light capture and photosynthesis of the plants that were under management regimes (chapter 4 and 5), was calculated instantaneously. During the day the intensity of the incoming light varies and it also depends on the geographical position. Day length, which is also related to the position on earth, is variable over a year. This affects the amount of light a plant receives and consequently plant growth. Also rain fall and soil characteristics may affect growth. If the model is to be used in ecosystems that are located far from the equator (for instance in temperate zones), or in systems that experience strong seasonal effects, or where water or soil factors greatly affect plant growth, it will need to be extended. However the model appeared to be useful in analysing ecological processes underlying growth of plants in a wet tropical forest. It provides an ecological solution to a practical problem and due to it easy-to-use character, it can be applied in the humid tropics to improve activities aiming at accelerating succession or improve species-site matching in enrichment planting schemes.

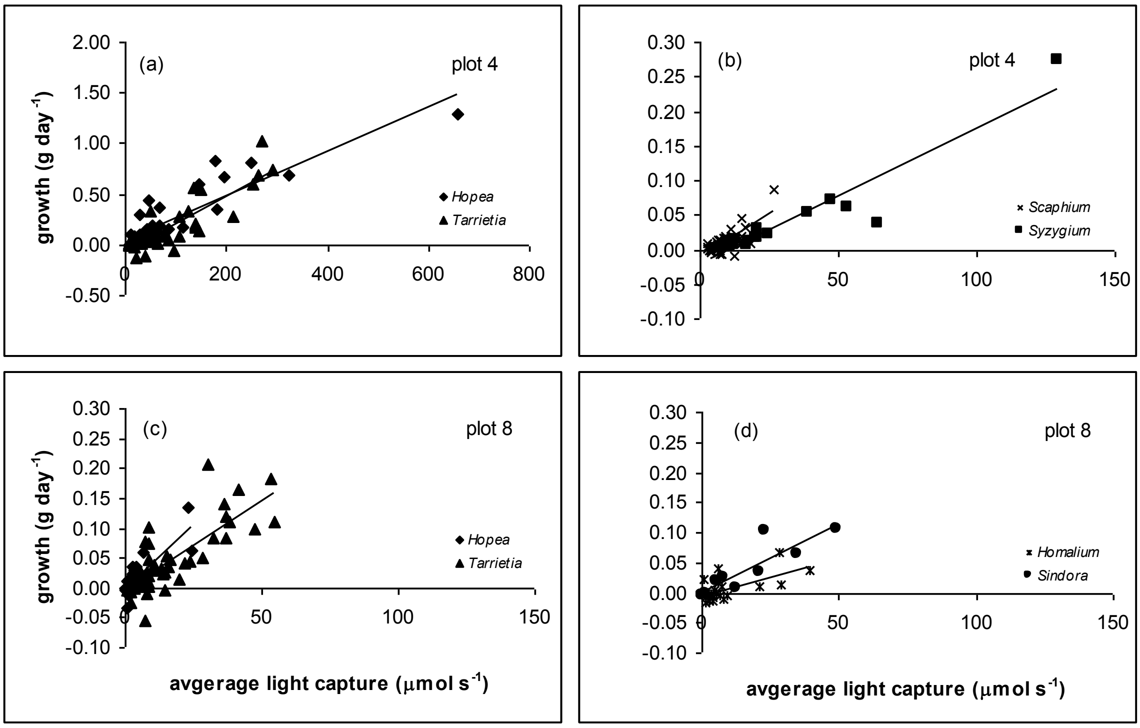

Fig. 2a-d Relation between observed growth and calculated light capture (average of the beginning and the end of the period in which growth was observed) of species planted in enrichment planting plots (plot 4 and 8) in Vietnam. All relations are significant (linear regression, $p<0.05$) and r^2 values vary from 0.5406 to 0.8893. For clarity two species per window are presented. Note the different scaling in window a.

Scope

The results of this study have shown that secondary succession is not necessarily steered by asymmetric light competition, in contrast to what is generally believed. I have shown how species can co-exist for at least five years by analysing ecological processes that underly plant growth. I showed that pioneers species can differ considerably from each other in functional traits when it comes to morphology and physiology (SLA, dark respiration, light compensation point, resorption, leaf life span), but that this does not result in large differences in relative growth rates or in large changes in size hierarchy during early succession.

The model presented in this dissertation has a large potential in the area of restoration ecology. Here it was applied in an experiment in which pioneers were liberated and in enrichment plantings in natural vegetation, but it could be applied in many more situations. It will be very useful in analysing growth patterns of trees subjected to different management practices and this will contribute to improve the success of activities aimed at accelerating forest regeneration.

Taking a break!

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Measuring leaf area

Samenvatting

Nadat landbouwgrond is verlaten begint de regeneratie van een bos. De vegetatie die dan ontstaat noemen we secundair bos. Gewoonlijk wordt de vegetatie eerst gedomineerd door niet-houtige planten en struiken, die na enkele jaren worden vervangen door pionierbomen. Na enkele decennia sterven de pioniers af en krijgen de climaxsoorten de kans om door te groeien en samen vormen ze later het bos. Dit proces, waarbij soorten elkaar opvolgen in de tijd, heet successie en is de natuurlijke manier waarop een bos zich herstelt. Vaak stagneert dit herstelproces echter al tijdens vroege stadia van successie. Niet-houtige planten en struiken groeien hard na verstoring en worden dominant, waardoor jonge bomen niet voldoende licht krijgen om te groeien. Wat overblijft is een struiklandschap van weinig biologische, economische, sociale en culturele waarde.

Vooral in de Tropen zijn mensen afhankelijk van de diensten en producten die door het bos worden geleverd. Omdat het areaal aan secundair bos daar snel toeneemt, worden secundaire bossen voor mensen steeds belangrijker om in hun levensonderhoud te voorzien. Daarom is het belangrijk om te begrijpen hoe het proces van bosregeneratie verloopt. Recentelijk is er veel aandacht voor beheersmaatregelen die erop gericht zijn de regeneratie van bossen te versnellen en te verbeteren (bosherstel).

Deze studie combineert fundamenteel en toegepast onderzoek. Het fundamentele deel behandelt de natuurlijke regeneratie van bos. De focus ligt daarbij op concurrentie om licht en de efficiëntie van het gebruik van stikstof en hoe deze factoren van invloed zijn op het succes van soorten tijdens de vroege stadia van successie. Het toegepaste deel behandelt twee beheersmaatregelen die regelmatig voor bosherstel worden gebruikt: het vrijhakken van gewenste boomsoorten zodat deze meer licht krijgen en sneller groeien en het verrijken van een bos door aanplantingen met gewenste soorten.

De rol van concurrentie om licht en stikstofgebruik tijdens natuurlijke regeneratie

Tijdens het regeneratieproces neemt de vegetatie in hoogte toe. Hoge planten hebben het voordeel dat zij hun blad in hoger gelegen, lichtere lagen van het bladerdek van de vegetatie kunnen plaatsen waardoor zij voldoende licht kunnen invangen om te overleven en te groeien en tegelijkertijd hun kleinere buren kunnen overschaduwen. Vaak wordt gedacht dat deze hoge planten meer licht invangen in verhouding tot hun biomassa (Φ_{mass}) dan kleinere planten en dat zij daardoor, in vergelijking met hun kleinere buren, sneller kunnen groeien. Zij zouden kleinere planten door hun snellere groei wegconcurreren en dit zou in grote mate de soortensamenstelling van een bos bepalen. Of dit proces daadwerkelijk plaatsvindt, was echter tot nu toe nog niet kwantitatief bepaald.

De groeisnelheid en de grootte van een plant wordt niet alleen door zijn lichtinvang per eenheid biomassa (morfologie) bepaald, maar ook de efficiëntie waarmee licht gebruikt wordt om te fotosynthetiseren (LUE) (fysiologie) heeft invloed op de groei. Een combinatie van morfologische en fysiologische eigenschappen bepaalt dus het succes van een plant tijdens regeneratie. In deze studie is voor het eerst bestudeerd in welke mate lichtinvang gerelateerd aan plantgrootte en LUE, invloed hebben op de groei van planten over de tijd, gemeten aan dezelfde planten in een secundair tropisch bos tijdens de eerste jaren van successie.

In hoofdstuk 2 gebruik ik een model waarmee een verband gelegd kan worden tussen de morfologische als fysiologische eigenschappen van een individuele plant en de daaraan gerelateerde lichtinvang en fotosynthese. Ik heb bomen in jonge successiestadia bestudeerd om te zien welke factoren bepalen of een soort succesvol wordt of niet. Ik heb individuen van een struik en drie boomsoorten geselecteerd en heb deze gedurende een tijdsperiode gevolgd (van een half jaar tot een 1,5 jaar oud bos, een 5 jaar oud bos is apart bestudeerd). Het bleek dat, in tegenstelling tot wat veelal wordt gedacht, lichtinvang per eenheid biomassa niet in grote mate bepaalt of een plant dominant wordt. Hoge planten hebben geen hogere lichtinvang per eenheid biomassa dan kleinere planten. Ook LUE was niet gerelateerd aan plantgrootte.

Evenveel lichtinvang per eenheid biomassa en gelijke LUE maken het mede mogelijk dat soorten tijdens regeneratie naast elkaar kunnen bestaan, zoals in het door mij onderzochte bos. Hierdoor is ook de groei van bomen in verhouding tot hun biomassa voor soorten en voor individuen binnen een soort nagenoeg gelijk. Mede als gevolg hiervan bleef de soortensamenstelling van dit bos in ieder geval gedurende 5 jaar constant. In latere stadia zullen de kleinere soorten en individuen niet overleven, want zij zijn architectonisch gelimiteerd om de hoogte in te groeien. De vegetatie zal steeds dichter worden waardoor lichtbehoevende soorten zullen verdwijnen en schaduwtolerante soorten zullen blijven groeien. Daardoor zal de soortensamenstelling van dit bos veranderen.

Naast lichtinvang en –gebruik kan ook stikstofgebruik invloed hebben op de concurrentieverhouding tussen planten. Stikstof is een essentiële bouwstof voor eiwitten die betrokken zijn bij het fotosyntheseproces. Omdat de beschikbaarheid gelimiteerd is en de opname ervan energie kost, is het belangrijk voor een plant stikstof efficiënt te gebruiken voor groei. Deze efficiëntie hangt van morfologische eigenschappen van een plant af, zoals zijn hoogte, kroondimensies, bladoppervlak, maar ook van eigenschappen zoals bladlevensduur, stikstofresorptie en andere fysiologische eigenschappen. In hoofdstuk 3 ontwikkel ik een model, gebaseerd op een al bestaand concept, waarmee ik bovengenoemde planteigenschappen kan relateren aan stikstofgebruik. Er bleken grote verschillen in de efficiëntie van stikstofgebruik tussen soorten te zijn, maar dit was niet aan hun dominantie in de vegetatie gerelateerd. Verschillen waren vooral te wijten aan de verschillen in bladlevensduur en stikstofresorptie. Een hoge bladlevensduur en een hoge resorptie lijken op een gedegradeerde bodem, zoals die waarop dit onderzoek werd gedaan, zeer nuttige eigenschappen te zijn.

Door de relatief langzame ontwikkeling van de vegetatie in dit onderzoek, kunnen alle planten het regeneratieproces ‘bijhouden’. Zij kunnen zich morfologisch en fysiologisch voldoende aan de veranderingen in de vegetatie aanpassen om te blijven bestaan, in ieder geval gedurende de eerste 5 jaar van bosregeneratie. Gezien de resultaten van hoofdstuk 2 en 3 lijkt het waarschijnlijk dat in dit bos de initiële zaailinggrootte de grootte van de planten later in successie bepaalt. Initiële zaailinggrootte wordt door zaadgrootte, efficiënt gebruik van de voedingsstoffen in het zaad of door kleine verschillen in het tijdstip van kieming bepaald.

Bosherstel

De natuurlijke regeneratie van een tropisch bos is vaak langzaam of wordt in zijn geheel gehinderd doordat niet-houtige planten en struiken in de eerste fase van successie overdadig groeien en daardoor te sterke concurrenten zijn voor bomen. Ook vatten zij snel vlam waardoor jonge bomen door het vuur vernietigd worden.

Twee vaak toegepaste beheersmaatregelen om regeneratie te versnellen zijn het vrijkappen van gewenste bomen zodat zij sneller groeien en het aanplanten van gewenste boomsoorten. In deze studie heb ik het PHOLIAGE-model gebruikt waarbij ik fundamentele ecologische processen die ten grondslag liggen aan boomgroei, op een kwantitatieve manier analyseer, zodat praktische problemen gerelateerd aan bosherstel benaderd kunnen worden.

Het vrijhakken van bomen resulteert over het algemeen in een toename in groei, zo ook in het experiment dat ik uitvoerde met pionierbomen in een 1,5 jaar oude vegetatie (zie hoofdstuk 4). De groei steeg met 34-49%, afhankelijk van de soort. De reactie op een opening in de vegetatie verschilde per soort, en dit heeft te maken met boomhoogte (t.o.v. de hoogte van de vegetatie), bladoppervlak, kroondimensies en de mate waarin de bomen lichtbehoevend zijn. De ideale grootte van de opening die in de vegetatie moet worden gecreëerd is dus verschillend voor elke soort, maar hangt ook van de hoogte en de dichtheid van de vegetatie af, dus van de leeftijd van het bos. In dit bos is het beter om in vroege stadia bomen vrij te hakken, omdat dit tot een grotere toename in groei leidt dan wanneer later wordt vrijgehakt en het zal minder arbeid kosten, want kappen in een jong bos is aanzienlijk makkelijker te doen dan in een hoger en dichter bos. Het PHOLIAGE-model kan de groei van bomen nauwkeurig voorspellen. Zo kan per boom en per bos bepaald worden wat het beste tijdstip is, wat de beste opening is en wat de effecten zijn van vrijhakken.

Wanneer bomen zijn vrijgehakt verandert vaak het patroon van biomassa-allocatie. Er wordt minder in hoogte geïnvesteerd maar des te meer in bijvoorbeeld kroonwijdte en kroondichtheid. Dit is belangrijk in jonge stadia want zo kunnen bomen eerder struiken en andere ongewenste planten wegconcurreren door meer schaduw op de bosvloer beneden zich te werpen. Dit versnelt bosregeneratie aanzienlijk.

Met dezelfde modelbenadering heb ik in hoofdstuk 5 boomgroei van zaailingen bestudeerd die in twee jonge bospercelen zijn aangeplant. In één van deze percelen zijn lijnen opengekapt waarin de zaalingen zijn geplant terwijl in het andere perceel de vegetatie intact bleef. De percelen verschillen in leeftijd en dus in dichtheid en hoogte. De verschillen in groei tussen de aangeplante soorten waren aan hun hoogte, bladoppervlak, kroondimensies en de mate waarin ze lichtbehoevend zijn gerelateerd. De verschillen tussen de percelen waren aan de verschillen in lichtklimaat tussen beide percelen gerelateerd. Dus het succes van de beheersmaatregelen hangt van de geselecteerde boomsoorten af en van het bos waarin zij geplant zijn. Met het model heb ik onderzocht wat er gebeurt als er in beide percelen meer licht voor de aangeplante zaailingen beschikbaar zou komen.

Over het algemeen gaven de berekeningen aan dat meer schaduwtolerante soorten sneller fotosynthesesnelheden (maat voor groei) die dicht bij hun maximum haalbare snelheden lagen kunnen bereiken, dan de meer lichtbehoevende soorten. Zij kunnen met een kleinere opening in de vegetatie (lijnbreedte of uitdunnen van het kronendak) volstaan dan de meer lichtbehoevende soorten. Het is echter niet altijd wenselijk om de vegetatie zodanig te openen zodat soorten maximale groei bereiken. In sommige gevallen moet een bos dan namelijk zodanig worden opengekapt dat het al bestaande bos ernstig vernield wordt. Daarnaast kost het veel arbeid, vooral als het bos groot is, of een grote dichtheid heeft of moeilijk bereikbaar is. Daarbij kunnen, bij een grote toename in lichtbeschikbaarheid, grassen gaan hergroeien. Met het model dat ik gebruik kan per boom berekend worden hoeveel de toename in groei is bij een bepaalde lijnbreedte gekapt in een bepaald bos, of bij een bepaalde mate van uitdunnen van het kronendak. Een kleinere lijnbreedte of kleine mate van uitdunnen kan ook al voor een grote toename in groei van de aangeplante bomen zorgen en zo kan op vernieling in het al bestaande bos en op arbeid bespaard worden. De beste beheersmaatregel kan gekozen worden, waarbij met zowel boomgroei als de hoeveelheid arbeid rekening wordt gehouden.

Er worden veel experimenten gedaan waarbij bomen worden vrijgekapt en waarbij bossen met aanplantingen worden verrijkt. Deze experimenten kosten veel tijd en geld en zijn wat betreft het aantal gerealiseerde groei-omstandigheden en herhalingen beperkt. Ik heb laten zien dat met een lichtmodel, fotosynthesesnelheden van dergelijke bomen berekend kunnen worden en dat de verkregen waarden goed correleren met de groei die ik in het veld heb waargenomen. Dat betekent dat dit model geschikt is om het effect van verschillende beheersmaatregelen op boomgroei te onderzoeken. Zo kunnen aanbevelingen worden gedaan over welke maatregel het beste is, rekening houdend met de eigenschappen van de gewenste boom en het bos waarin de boom groeit. Dit reduceert de noodzaak om langdurende en dure experimenten uit te voeren aanzienlijk.

Mogelijke toepassingen en gebruik van het model

In deze studie heb ik het PHOLIAGE-model toegepast in een experiment waarbij pioniers zijn vrijgekapt en in een jong bos waarin bomen zijn aangeplant. Het model is echter potentieel in veel meer situaties toepasbaar. Bijvoorbeeld in een ouder bos, waarin de groei van latere soorten zou moeten worden gestimuleerd om regeneratie te versnellen. Of in situaties waarbij bomen worden vrijgekapt of aangeplant, met een achterliggend economisch doel. De effecten van beheersmaatregelen op boomgroei kunnen worden gesimuleerd en zo kan worden berekend wat de meeropbrengst van bepaalde beheersmaatregelen zal zijn, rekening houdend met de kosten van de maatregel.

Het kan ook worden toegepast in situaties waarbij inheemse soorten onder het kronendak van exotische soorten worden aangeplant, zoals regelmatig gebeurt in de Tropen. Vaak worden deze exoten geplant omdat zij snel groeien en dus snel grassen kunnen wegconcurreren en bodemerosie kunnen voorkomen. Later worden inheemse soorten onder de exoten geplant om het bos te verrijken. Vóór het planten wordt vaak het kronendak uitgedund om er een beter lichtklimaat onder te creëren. Met het model dat in deze studie gepresenteerd wordt kan worden bestudeerd welke soorten in welk lichtklimaat het beste zullen groeien en welke beheersmaatregelen er nodig zullen zijn om de groei te vergroten. Dit zal het succes van dergelijke aanplantingsprojecten verhogen.

Het PHOLIAGE-model is niet het enige 3-D model dat fotosynthesesnelheden van individuele bomen kan berekenen, maar het is wel uniek in de toepassing om praktische problemen te benaderen die men bij bosherstel tegenkomt. De data die nodig zijn om dit model te gebruiken zijn relatief gemakkelijk te verzamelen en de enige benodigde software voor toepassing van het model is Excel. Als er geen mogelijkheden zijn om fotosynthesemetingen te doen, dan kan lichtinvang ook als maat voor plantgroei gebruikt worden (zie hoofdstuk 6). Het model heeft dus grote potentie in het vakgebied van bosherstel in de natte Tropen. Het kan bijdragen aan het succes van beheersmaatregelen die erop gericht zijn regeneratie van bossen te versnellen.

Harvesting saplings

Tóm tắt bằng tiếng Việt Nam (chương 6)

Diện tích rừng thứ sinh đang phát triển mạnh mẽ ở các vùng nhiệt đới. Rừng thứ sinh được hình thành sau khi rừng nguyên sinh bị tàn phá hoặc sau khi các diện tích canh tác nông nghiệp bị bỏ hoang. Đầu tiên, cây cỏ, cây bụi, dây leo xuất hiện, rồi tới sự có mặt của các loài cây tiên phong. Trong giai đoạn diễn thế tiếp theo, các loài sinh trưởng dưới tán xuất hiện và chiếm ưu thế khi các loài cây tiên phong chết đi ((cf. Finegan 1984; Peña-Claros 2003). Tuy nhiên, thực tế cho thấy có rất nhiều rừng thứ sinh không bao giờ đạt được giai đoạn đỉnh điểm của diễn thế. Nguyên nhân là do khi các loài cây bụi, cây cỏ và dây leo sinh trưởng, phát triển quá mức ở giai đoạn đầu của diến thế, gây cạnh tranh mãnh liệt và hạn chế sinh trưởng của các loài cây tiên phong và điều này cản trở rất lớn tới quá trình diễn thế của rừng (Aide et al. 1995; Nykvist 1996; Woods 1989).

Khi mà rừng nguyên sinh đang bị mất đi nhanh chóng (Hirsch 1997) thì rừng thứ sinh trở nên quan trọng. Ngày càng có nhiều người, đặc biệt là những người nghèo phụ thuộc vào nguồn tài nguyên của rừng thứ sinh, và do vậy việc tìm hiểu quá trình diễn thế của rừng thứ sinh là rất quan trọng. Hiện nay đã có khá nhiều các phương án nhằm quản lý và thúc đẩy tái sinh ở rừng thứ sinh nhiệt đới (Holl and Kapelle 1999).

Trong nghiên cứu này, tác giả kết hợp nghiên cứu cơ bản với nghiên cứu ứng dụng diễn thế rừng thứ sinh nhiệt đới. Phần nghiên cứu cơ bản tập trung vào vấn đề tái sinh tự nhiên của rừng. Các cá thể của các loài cây khác nhau được xem xét, nghiên cứu từ giai đoạn diễn thế ban đầu. Mối quan hệ giữa cạnh tranh ánh sáng (chương 2) và sử dụng nitơ hiệu quả (chương 3) tới sinh trưởng của cây cũng được xem xét. Phần nghiên cứu ứng dụng tập trung vào hai phương pháp thường được sử dụng trong phục hồi rừng là: luỗng phát dây leo bụi rậm và mở tán (chương 4) và làm giầu rừng (chương 5).

Vai trò của cạnh tranh ánh sáng và sử dụng nitơ hiệu quả

Chiều cao của thực vật tăng lên trong quá trình diễn thế. Tán lá của các cây cao có khả vươn rộng để thu nhận được nhiều ánh sáng hơn các cây thấp ((Givnish 1982). Nhìn chung, các cây cao có khả năng thu nhận được nhiều ánh sáng hơn các cây thấp (Ford 1975; Schwinning and Weiner 1998). Sự thu nhận ánh sáng không đồng đều giữa các cá thể cây rừng là do sự lớn lên không đồng đều về chiều cao giữa chúng trong quá trình diễn thế (Huston and Smith 1987; Van Breugel 2007). Các cây cao do thu nhận được nhiều ánh sáng sẽ sinh trưởng nhanh hơn và cao hơn, và do vậy chèn ép các cây thấp hơn và điều này có thể dẫn tới việc thay đổi thành phần loài cây. Tuy nhiên, vẫn chưa có nhiều nghiên cứu về mức độ cạnh tranh ánh sáng giữa các cá thể cây rừng (Aan et al. 2006; Anten and Hirose 1998; 1999; Hirose and Werger 1995; Werger et al. 2002), và chỉ có một nghiên cứu được tiến hành ở rừng thứ sinh nhiệt đới (Selaya et al. 2007).

Thu nhận ánh sáng đứng riêng rẽ không quyết định sinh trưởng của thực vật. Sử dụng ánh sáng hiệu quả cho quá trình quang hợp mới thực sự quan trọng đối với sinh trưởng của cây rừng (Hikosaka et al. 1999; Schwinning 1996). Sử dụng ánh sáng hiệu quả (LUE) được xác định bởi đặc tính sinh lý của thực vật như tốc độ quang hợp tối đa, hiệu suất quang hợp và hô hấp. Luận văn này là công trình đầu tiên nghiên cứu tương quan giữa thu nhận ánh sáng và kích thước thực vật và việc sử dụng ánh sáng hiệu quả tới sinh trưởng của các cá thể cây rừng ở rừng thứ sinh.

Trong chương 2 tôi nghiên cứu về cạnh tranh ánh sáng giữa một loài cây bụi thân gỗ và 3 loài cây gỗ, và tương quan giữa khả năng cạnh tranh ánh sáng với kích thước của thực vật thu thập được trong 5 năm đầu của quá trình diễn thế. Kết quả cho thấy bốn loài có các giá trị gần tương tự nhau về mức độ thu nhận ánh sáng trên một đơn vị sinh khối trên mặt đất (Φ_{mass}) và sử dụng nitơ hiệu quả (LUE) mặc dù có sự khác nhau về chiều cao trung bình giữa các loài. Nhìn chung các loài cây cao hơn thu nhận ánh sáng nhỉnh hơn trên một đơn vị diện tích lá (Φ_{area}), nhưng do sự khác biệt giữa diện tích lá trên đơn vị sinh khối là nhỏ (tỷ lệ diện tích lá: LAR), Φ_{mass} gần như tương đương giữa các loài cây cao và thấp và giữa các cá thể cao và thấp trong cùng loài (ghi chú là $\Phi_{mass}=\Phi_{area}$*LAR). Điều này trái với nhận thức chung là có sự thu nhận ánh sáng khác nhau, các loài cây cao thu nhận nhiều ánh sáng hơn. Kết quả nghiên cứu cũng phù hợp với một số nghiên cứu khác kết luận là các loài có kích thước khác nhau nhưng có Φ_{mass} tương tự nhau (Anten and Hirose 1999; Hirose and Werger 1995; Selaya et al. 2007). Hirose và Werger (Aerts and Van der Peijl 1993). Nitơ là một thành phần thiết yếu của protein quang hợp (Evans 1989) và do vậy sinh trưởng của cây sẽ bị giảm đáng kể nếu thiếu nitơ (Kachi and Hirose 1983; Vermeer and Berendse 1983). Như vậy, sử dụng nitơ hiệu quả cho sinh trưởng sinh khối có thể sẽ góp phần vào sự thành công của thực vật trong quá trình diễn thế (Ellsworth and Reich 1996; Herbert et al. 2004; van der Werf et al. 1993).

Sử dụng nitơ hiệu quả là đặc điểm chức năng thích ứng của cây bao gồm thời gian sống của lá, khả năng hút dinh dưỡng và nitơ của rễ, sử dụng nitơ hiệu quả ở quá trình quang hợp, và cũng quan trọng là chiều cao của cây, diện tích bề mặt lá và sự phân bố của nitơ. Tuy nhiên, có rất ít các nghiên cứu về mối quan hệ giữa các đặc điểm này với sử dụng nitơ hiệu quả ở cây. Trong nghiên cứu này, tôi đã sử dụng các khái niệm của Hiremath (2000) để nghiên cứu các mức độ sử dụng nitơ hiệu quả của tán cây ($PNUE_{cum}$), nghiên cứu các đặc điểm như chiều cao của cây (ví dụ vị trí tán lá), thu nhận ánh sáng của toàn bộ tán và phân bố của nitơ ở tán cây.

Ở chương 3, $PNUE_{cum}$ và các đặc điểm liên quan được xác định cho 4 loài ở 2 lâm phần khác tuổi, chiều cao và LAI, như đã được sử dụng ở chương 2. $PNUE_{cum}$ khác nhau giữa các loài. Sự khác nhau này không liên quan tới kích thước của loài ở lâm phần. $PNUE_{cum}$ là năng suất sản xuất nitơ quang hợp (PNP) và thời gian trung bình sử dụng nitơ (MRT). PNP không khác nhau giữa các loài trong lâm phần. Sự khác nhau về chiều cao giữa các loài có tương quan yếu và sự khác nhau về mức độ ánh sáng cũng có tương quan yếu (xem giá trị của Φ_{area} ở chương 2). Mặt khác, các thành phần xác định MRT, thời gian sống của lá và khả năng hút nitơ khác nhau rất lớn giữa các loài và tạo ra sự khác nhau về $PNUE_{cum}$.

MRT cao chắc chắn sẽ có lợi thế trong môi trường nghèo nitơ, nơi mà sử dụng tiết kiệm nitơ chứ không phải là sinh trưởng nhanh sẽ là chìa khoá cho sự tồn tại (Hiremath 2000). Một điều rõ ràng là ở đất nghèo dinh dưỡng các loài có MRT cao chứ PNP không được đánh giá cao (Aerts and de Caluwe 1994; Vazquez de Aldana and Berendse 1997; Yuan et al. 2005) mặc dù điều này chưa được thử nghiệm ở rừng thứ sinh nhiệt đới. Tại địa điểm nghiên cứu của chúng tôi đất bị thoái hoá do ảnh hưởng của chiến tranh và sau đó là một vài chu kỳ canh tác nương rẫy 5-6 năm với thời gian bỏ hoá rất ngắn (vài tháng) và như vậy việc sử dụng hiệu quả và tiết kiệm nguồn nitơ là rất hữu ích (xem dos Santos et al. 2006).

Nhìn chung thực vật sẽ sinh trưởng chiều cao mạnh mẽ khi chúng gặp tầng tán có nhiều ánh sáng hơn. Điều này làm tăng Φ_{area} và PNP. Sinh trưởng chiều cao được tạo bởi sự sinh trưởng nhanh của lá ở đỉnh tán sẽ giúp cây có lợi thế về cạnh tranh ánh sáng làm gia tăng quá trình quang hợp, sinh trưởng và phát triển (Boonman et al. 2006). Tuy nhiên, việc phân bố lá ở tầng trên của tán sẽ dẫn tới việc tầng lá bên dưới bị cắt giảm do khả năng cây tự điều chỉnh để sử dụng hiệu quả nguồn dinh dưỡng (Ackerly and Bazzaz 1995). Điều này làm tăng sự luân chuyển và giảm thời gian sống của lá. Thời gian sống ngắn của lá tầng dưới làm giảm thời gian sử dụng nitơ (MRT) và do vậy làm giảm khả năng sử dụng nitơ hiệu quả. Điều này có nghĩa là nếu khả năng thu nhận ánh sáng và PNP không giúp cây làm giảm MRT, việc sử dụng nitơ của cây sẽ giảm và cây sẽ sinh trưởng cao hơn. Điều này có thể ảnh hưởng tới sinh trưởng của cây đặc biệt là với sự thay đổi của nguồn nitơ trong quá trình diễn thế (Ewel et al. 1991). Các xu hướng này chưa được chú ý trong các nghiên cứu đã có. Sự phát triển của thực vật là tương đối chậm, cho phép loài thích nghi với điều kiện của lâm phần và sự thay đổi về ánh sáng. Do cấu trúc mở của thực vật, thu nhận ánh sáng và PNP không tăng cùng với chiều cao của cây.

Một điều được tìm ra là thực vật không thể cùng một lúc sử dụng tối đa nguồn nitơ và sử dụng hiệu quả ánh sáng (Hirose and Bazzaz 1998). Tuy nhiên, trong nghiên cứu này chúng tôi thấy các loài có LUE cao nhất cũng có $PNUE_{cum}$ cao nhất. Đây là loài có chiều cao thấp nhất trong bốn loài nghiên cứu nên có thể rút ra là sử dụng hiệu quả ánh sáng và nitơ cao không liên quan tới chiều cao của thực vật.

Kết quả của chương 2 và 3 cho thấy chiều cao của cây con ban đầu quyết định tới chiều cao của cây nhỡ tiên phong ở giai đoạn diễn thế tiếp theo (Boot 1996). Chiều cao cây con ban đầu được quyết định bởi kích thước của hạt và việc sử dụng hiệu quả năng lượng từ hạt để sinh trưởng chiều cao trong giai đoạn cây con, và một phần nhỏ do thời gian nảy mầm.

Sinh thái phục hồi rừng

Trong chương 2 và 3 tôi phân tích quá trình tái sinh dưới tán rừng tự nhiên. Như đã đề cập từ trước, tái sinh rừng tự nhiên thường diễn ra chậm hoặc hoặc khó khăn do bị cạnh tranh ánh sáng, nước và dinh dưỡng khoáng từ cây bụi, dây leo hoặc cây cỏ (Berkowitz et al. 1995; Holl 1998; Parrotta et al. 2002; Putz and Canham 1992) hoặc bị cháy ở mùa khô sẽ làm tổn hại tới cây tái sinh (Werger 1983). Điều này cản trở rất lớn tới quá trình diễn thế của rừng.

Hai phương pháp thường dùng để xúc tiến diễn thế là phát luỗng dây leo, bụi rậm và mở tán (gọi tắt là mở tán), và làm giầu rừng. Tôi sử dụng mô hình (PHOLIAGE) để phân tích kết quả của thí nghiệm mở tán ở lâm phần rừng thứ sinh 1,5 tuổi (chương 4). Phương pháp tương tự được sử dụng để phân tích sinh trưởng của cây bản địa trồng dưới tán 2 lâm phần rừng non do Vườn quốc gia Bạch Mã thực hiện và là một phần trong chương trình trồng mới 5 triệu ha rừng của Việt Nam (chương 5). Các đặc tính sinh thái cơ bản là nền tảng cho sinh trưởng của cây được phân tích để làm rõ các vấn đề nảy sinh trong quá trình xúc tiến diễn thế.

Khi sinh trưởng của cây tái sinh bị cạnh tranh mãnh liệt bởi cây xung quanh thì mở tán là phương pháp hiệu quả để thúc đẩy sinh trưởng của cây (Collet et al. 1998; Finegan et al. 1999) và do vậy thúc đẩy quá trình diễn thế. Mở tán cho các loài cây mục đích tiên phong ở lâm phần 1.5 tuổi sẽ làm tăng mức độ thu nhận ánh sáng và tốc độ quang hợp. Sinh trưởng có thể tăng 34-49% tuỳ thuộc vào từng loài cây, và liên quan tới chiều cao, diện tích lá, hình dạng tán lá và các đặc tính sinh lý như tốc độ quang hợp tối đa và hô hấp dưới tán.

Khoảng trống mà cây con tái sinh cần có để tối đa tốc độ quang hợp phụ thuộc vào nhu cầu ánh sáng của cây, và cũng phụ thuộc vào chiều cao và mật độ của cây rừng xung quanh. Ở giai đoạn đầu khi mà lâm phần được 0,5 tuổi, chiều cao và mật độ của lâm phần khá thấp, tốc độ quang hợp của cây tiên phong có thể tăng từ 164-207% nếu cây được phát luỗng dây leo, bụi rậm với bán kính 0,5 m. Ở giai đoạn kế tiếp (lâm phần được 1,5 tuổi) khi mà cây tiên phong vươn tới gần đỉnh tán của thực vật xung quanh thì phát luỗng dây leo bụi rậm ảnh hưởng kém hơn tới tốc độ quang hợp của cây. Do vậy, phát luỗng dây leo bụi rậm và mở tán ở giai đoạn đầu của diễn thế sẽ có tác dụng lớn nhất tới cây mục đích và cũng tốn ít nhân công nhất. Với mô hình PHOLIAGE, ta có thể nghiên cứu ảnh hưởng của mở tán đối với từng cá thể trong lâm phần rừng và có thể lựa chọn được phương án mở tán tốt nhất.

Khi sinh trưởng của cây không còn bị ảnh hưởng bởi thực vật xung quanh thì tỷ lệ sinh khối của cây thay đổi. Sinh trưởng của tán lá được phát triển mạnh thay thế cho việc giảm sinh trưởng về chiều cao (Collet et al. 1998). Điều này rất quan trọng trong các lâm phần ít tuổi khi bị cây bụi cạnh tranh, cây tái sinh luân phải sinh trưởng chiều cao để chiếm tầng ưu thế. Khi tán lá sinh trưởng dày hơn sẽ che bóng cây bụi và cỏ mọc ở dưới tán. Khi mà cây đã vươn lên tầng trên và dần che phủ cây xung quanh thì sinh trưởng của cây có thể bị giảm.

Mô hình cũng giúp nghiên cứu tương quan giữa tốc độ quang hợp của các loài cây bản địa trồng ở 2 lâm phần khác tuổi, chiều cao và LAI với tăng trưởng của cây. Các loài khác nhau về tốc độ quang hợp có thể do sự khác nhau về đặc điểm hình thái (chiều cao, diện tích lá, hình thái tán lá), và các đặc điểm sinh lý liên quan tới nhu cầu ánh sáng (mức độ chịu bóng). Các lâm phần khác nhau sẽ có điều kiện ánh sáng khác nhau.

Các cây chịu bóng có tốc độ quang hợp gần bằng với tốc độ tiềm năng khi chúng sinh trưởng ở các ô thí nghiệm. Khi mở tán cho cây sẽ làm tăng tốc độ quang hợp. Loài cây ưa sáng sẽ rất có lợi khi mở tán do chúng cần nhiều ánh sáng để đạt tốc độ quang hợp tối đa và có thể tăng hơn 40%. Tuy nhiên, việc mở tán cho cây cũng nên cân nhắc tới các điều kiện không mong muốn hoặc không thực tế. Ví dụ, việc tạo ra những băng chặt rộng 5 m cho cây Sao đen (*Hopea odorata*) sẽ làm cho cây có tốc độ quang hợp cao nhất. Tuy nhiên, việc này sẽ tốn rất nhiều công sức, tiền bạc, và cũng có thể làm tổn hại tới rừng. Bên cạnh đó, việc tạo ra các khoảng trống cũng có thể làm cho cỏ hoặc các loài cây không mong muốn có điều kiện sinh trưởng và cạnh tranh với cây tái sinh ((McNamara et al. 2006). Với băng chặt nhỏ hơn (2 m) sẽ ít làm tổn hại tới rừng hơn và cũng có thể làm tăng tốc độ quang hợp của Sao đen lên khoảng 30%. Khi mô hình bao gồm cả sinh trưởng của cây và số nhân công cần thiết sẽ cho phép tính toán và lựa chon phương pháp quản lý thích hợp nhất.

Đã có rất nhiều các thí nghiệm về mở tán và làm giàu rừng, nhưng chúng đòi hỏi về thời gian, không gian và tiền bạc, và các kết quả thường hạn chế ở các trường hợp cụ thể và nhìn chung chỉ dừng lại ở một số điều kiện thí nghiệm và một số lặp lại (Paquette et al. 2006). Trong chương 4 và 5 tôi đã dự đoán các đặc tính quang hợp của các loài cây mục đích dựa vào mô hình toán được thiết lập dựa trên các số liệu thu thập được. Điều này chỉ ra rằng mô hình toán này có thể giúp dự đoán sinh trưởng của cây tái sinh tự nhiên hoặc trồng ở các giai đoạn diễn thế ban đầu. Các biện pháp kỹ thuật phổ thông như phát luỗng dây leo, bụi rậm, trồng theo hàng và tỉa thưa tán cây chèn ép có thể được áp dụng với thời gian và cường độ thích hợp. Bằng cách này, các hoạt động quản lý có thể được áp dụng với hiệu quả cao hơn và cũng giảm được nhu cầu thực hiện các thí nghiệm dài và tốn kém.

Tiềm năng áp dụng mô hình

Trong nghiên cứu này mô hình PHOLIAGE được áp dụng trong một thí nghiệm mà cây tiên phong được mở tán và trong hai lâm phần rừng tự nhiên. Tôi cho rằng mô hình này có thể được áp dụng ở những nơi cần thiết phải mở tán, ví dụ ở rừng già hơn và sinh trưởng của các loài cây ưu thế cần được cải thiện để thúc đẩy diễn thế. Nó cũng có thể áp dụng việc mở tán hoặc trồng làm giầu rừng ở những nơi có điều kiện kinh tế (De Graaf et al. 1999; Guariguata 1999). Ảnh hưởng của các biện pháp quản lý khác nhau tới sản xuất gỗ và lợi ích có thể được tính toán.

Một ví dụ nữa có thể áp dụng mô hình là làm giàu rừng trồng. Thông thường ở Đông Nam Á, các vùng đất thoái hoá thường bị các loài không mong muốn xâm lấn như loài cỏ *Imperata cylindrica* (McNamara et al. 2006; Otsamo et al. 1997). Các loài cây nhập nội sinh trưởng nhanh được nhập và gây trồng để chống xói mòn và nhanh tạo tán để diệt trừ cỏ dại. Khi tán cây giao nhau thì cỏ dại bị loại trừ, và cây bản địa được trồng dưới tán để làm giàu lâm phần (McNamara et al. 2006; Otsamo 2000). Thường là tán cây được tỉa vào lúc trồng hoặc sau khi trồng cây bản địa để tăng ánh sáng cho các cây con (McNamara et al. 2006; Otsamo 1998). Tuy nhiên, do không biết rõ mức độ ảnh hưởng của tỉa thưa tới sinh trưởng của cây nên công việc này thường được tiến hành qua cách THỬ & HỎNG, và rõ ràng là gây nhiều lãng phí tới thời gian và kinh phí thực hiện.

Một ví dụ về nơi phương pháp này được thực hiện là ở khu vực Hải Vân, phía nam của Phú Lộc, Thừa Thiên Huế (McNamara et al. 2006). Sau chiến tranh đã có rất nhiều các khu rừng bị tàn phá và bị xâm lấn bởi loài cỏ (*I. cylindrica*), và kết quả là rừng không thể phục hồi. Năm 1986, loài Keo lá tràm (*Acacia auriculiformis)* được nhập và trồng với các mật độ khác nhau và chúng chèn ép cỏ dại khi được vài năm tuổi. Tầng tán trên của Keo được tỉa vào giữa năm 1993 và 2000 khi cây bản địa được trồng dưới tán. Do cường độ tỉa thưa lần đầu quá lớn tạo nên điều kiện thuận lợi cho các loài cỏ sinh trưởng và cạnh tranh mãnh liệt với cây bản địa. Lần tỉa thưa thứ 2 có cường độ nhỏ hơn.

Do Keo được trồng với mật độ khác nhau và mức độ tỉa thưa cũng khác nhau nên cường độ ánh sáng tới cây con bản địa trồng dưới tán cũng khác nhau. Lúc đầu có rất nhiều các loài cây bản địa (khoảng 40 loài) được trồng dưới tán Keo nhưng phần lớn đã bị chết, và các đợt trồng tiếp theo chủ yếu đối với một số loài sống sót (khoảng 13 loài). Nhìn bề ngoài loài kém phù hợp với lập địa. Mô hình trình bày trong luận văn này có thể đóng góp vào sự thành công của việc trồng làm giàu dưới tán rừng, bằng cách phân tích ảnh hưởng của các biện pháp kỹ thuật khác nhau với mức độ ánh sáng thu được tới tốc độ quang hợp của cây trồng.

Sử dụng mô hình PHOLIAGE

Mô hình PHOLIAGE chỉ là một trong các mô hình 3 chiều tính toán tốc độ quang hợp của cây, nhưng lại là mô hình duy nhất được sử dụng để giải quyết các vấn đề nảy sinh của sinh thái phục hồi. Số liệu để xây dựng mô hình có thể thu thập đơn giản và nhanh so với các mô hình khác đòi hỏi số liệu chi tiết và phức tạp hơn (Pearcy and Yang 1996; Sterck and Schieving 2007). Số liệu về ánh sáng thu thập bằng máy đo ánh sáng có độ tin cậy cần thiết (chương 4 và 5). Thu thập số liệu về mô hình mở tán hoặc làm giàu rừng cũng dễ dàng do có rất nhiều loài cây được trồng ở các vùng rộng lớn. Trở ngại lớn nhất là đo tốc độ quang hợp do phải sử dụng thiết bị rất đắt tiền. Ở các nước nhiệt đới, việc đo đếm các đặc tính quang hợp thường gặp khó khăn do thiếu kinh phí và con người. Nhưng mức độ thu nhận ánh sáng của tán cây có mức tương quan chặt với sinh trưởng của cây (Hình 1 & 2), do vậy trong trường hợp không thể đo được tốc độ quang hợp thì có thể sử dụng số liệu về thu nhận ánh sáng của tán lá. Số liệu về cây mục đích và cây xung quanh nhập vào các trang số liệu của Excel có thể được sử dụng dễ dàng trong mô hình. Kết quả đầu ra của mô hình là ánh sáng thu nhận của tán lá và tốc độ quang hợp của mỗi một cá thể cây rừng.

Trong nghiên cứu này, thu nhận ánh sáng và quang hợp của thực vật ở các biện pháp tác động (chương 4 & 5) được tính toán nhanh. Ban ngày, cường độ ánh sáng khác nhau theo thời gian và nó cũng phụ thuộc vào vị trí địa lý. Thời gian của ngày cũng phụ thuộc vào vị trí địa lý và thay đổi giữa các thời gian của năm. Điều này ảnh hưởng tới lượng ánh sáng mà cây thu nhận và qua đó ảnh hưởng tới sinh trưởng của cây. Lượng mưa và độ phì đất cũng có thể ảnh hưởng tới sinh trưởng của cây. Nếu sử dụng mô hình ở các hệ sinh thái cách xa đường xích đạo (ví dụ vùng ôn đới), hoặc hệ sinh thái ở nơi có các mùa khác nhau rõ rệt, hoặc nơi mà đất và nước có ảnh hưởng rất lớn tới sinh trưởng của cây, mô hình cần được mở rộng hơn. Tuy nhiên, mô hình rất hữu ích trong phân tích các quá trình sinh thái ảnh hưởng tới sinh trưởng của thực vật dưới tán rừng nhiệt đới ẩm. Nó đưa ra giải pháp sinh thái cho các vấn đề thực tiễn nảy sinh, nó có thể được áp dụng ở các vùng nhiệt đới ẩm để xúc tiến diễn thế hoặc cải thiện việc lựa chọn loài phù hợp với lập địa cho trồng làm giàu rừng.

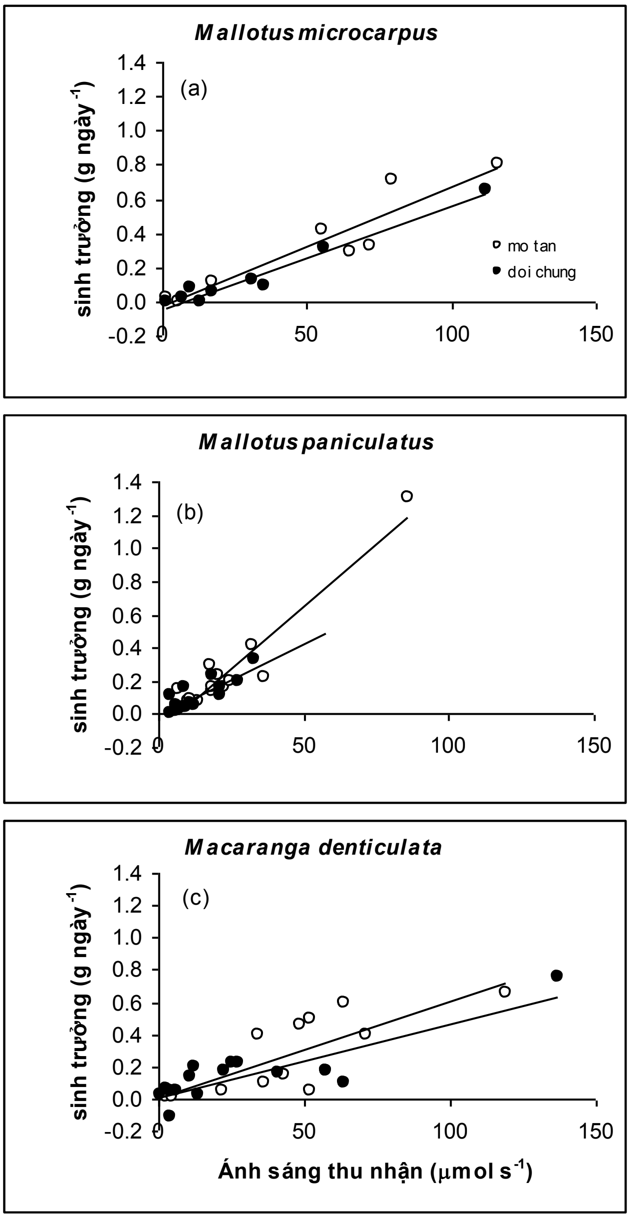

Fig. 1a-c Tương quan giữa sinh trưởng sinh khối trên mặt đất của cây sau khi thảm tươi, cây bụi bị chặt bỏ được 174 ngày và ánh sáng thu nhận được ngay sau khi thảm tươi, cây bụi bị loại bỏ. Tất cả các tương quan đều có ý nghĩa (MM, $p<0.05$) và hệ số r^2 biến động từ 0.6498 tới 0.9635.

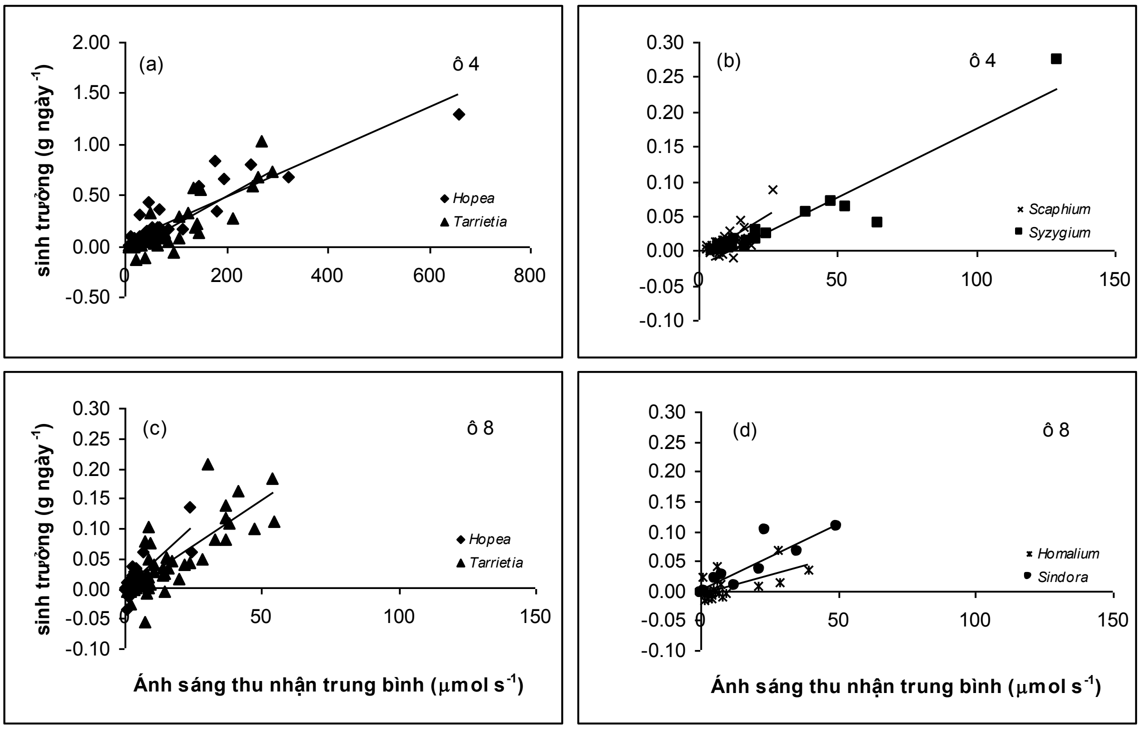

Fig. 2a-d Tương quan giữa sinh trưởng của cây và ánh sáng thu nhận (giá trị trung bình đo được ở thời gian trước và sau của quá trình) của loài làm giàu rừng ở các ô thí nghiệm ở Vietnam (ô 4 và 8). Tất cả các tương quan đều có ý nghĩa (hồi quy tuyến tính, $p<0.05$) và hệ số r^2 biến động từ 0.5406 tới 0.8893. Mỗi một hình vẽ được trình bày 2 loài, và hình vẽ a có tỷ lệ khác so với các hình còn lại.

Giới hạn

Kết quả của nghiên cứu này chỉ ra rằng diễn thế thứ sinh không bị ảnh hưởng nhiều bởi cạnh tranh ánh sáng, và điều này ngược lại với nhận thức chung của chúng ta. Tôi cũng đã trình bày cách thức mà các loài có thể chung sống, ít nhất là trong thời gian 5 năm bằng cách phân tích quá trình sinh thái ảnh hưởng tới sinh trưởng của thực vật. Tôi thấy các loài tiên phong khác nhau về các đặc tính chức năng thể hiện ở đặc điểm hình thái và sinh lý (SLA, hô hấp dưới tán, điểm sử dụng ánh sáng, khả năng thẩm thấu, thời gian sống của lá) khác nhau, nhưng điều này lại không ảnh hưởng tới việc thu nhận ánh sáng hiệu quả của cây.

Mô hình trình bày trong luận văn có tiềm năng áp dụng rộng rãi trong lĩnh vực sinh thái phục hồi. Trong nghiên cứu này, mô hình được áp dụng ở thí nghiệm các loài cây tiên phong được mở tán và các loài cây bản địa được trồng làm giàu dưới tán rừng thứ sinh, nhưng nó cũng có thể được áp dụng cho các trường hợp khác. Sẽ rất hữu ích nếu có thể nghiên cứu, phân tích sinh trưởng của cây dưới các biện pháp tác động khác nhau, vì điều này sẽ góp phần vào thành công của việc xúc tiến tái sinh ở rừng tự nhiên.

After tyfoon Xangsane (September-October 2006)

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The years that I spent in Vietnam have been the most fascinating in my life so far. It sure was not always easy working in a country that is so different from the country I was used to, but it has left me with many indispensable and valuable experiences that have broaden my horizons even further. I feel privileged to have been given the opportunity to live and work in such a beautiful country, one that I have greatly enjoyed!

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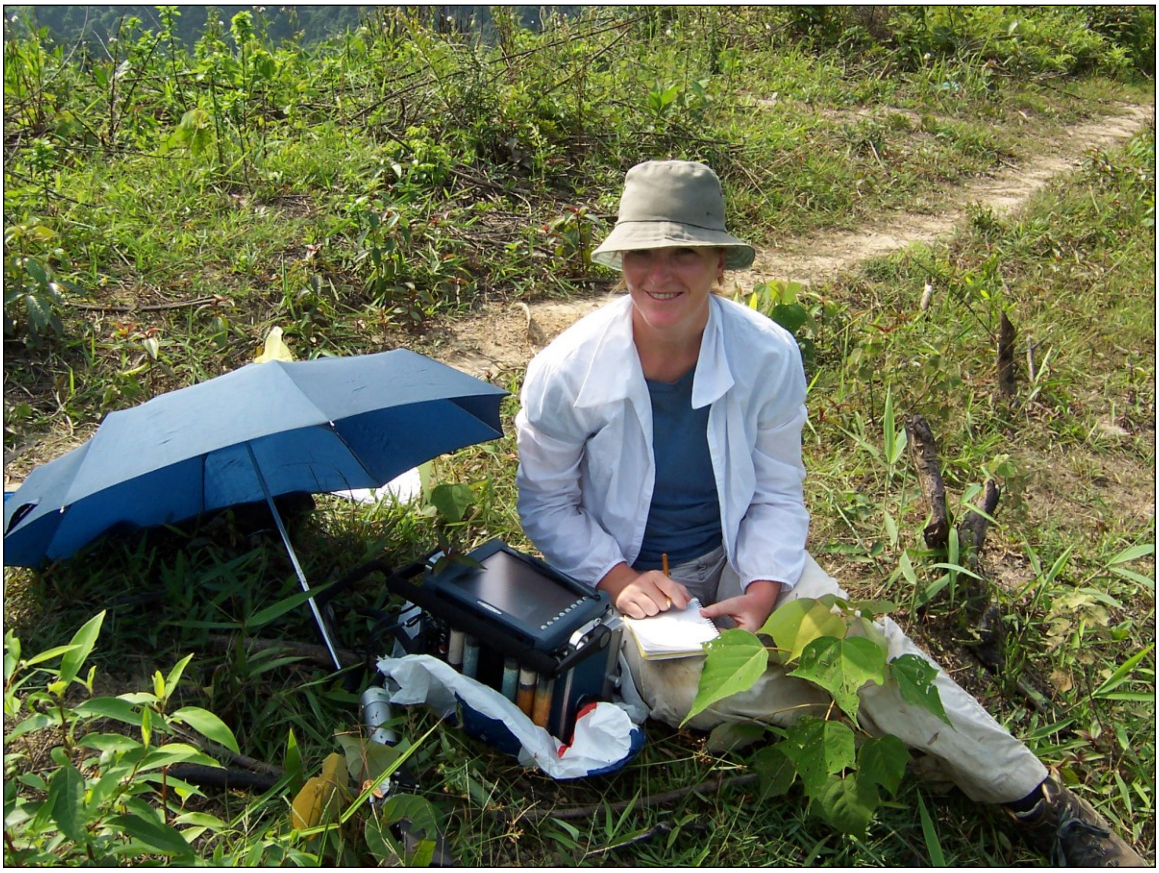
Curriculum Vitae

I was born on June 27th 1979 in Nijmegen, the Netherlands. From 1991 until 1997 I attended secondary school at the Over-Betuwe College in Bemmel. I started my study in Biology at the Radboud University Nijmegen in 1997, but I also followed courses at Wageningen University and Utrecht University. My first internship (including a field trip to Israel) was done at the joint geology department of Nijmegen and Utrecht, after which I conducted research on biological water purification in Uganda (within the framework of IHE, Delft). The third internship was done at the Plant Ecology & Biodiversity Group of Utrecht University in Bolivia, on seed dispersal of *Bertholletia excelsa*. In 2002 I obtained my Msc. degree from the Radboud University Nijmegen. In the same year I started working at IHE, Delft, as assistant teacher. In 2003 I started working as a policy advisor at the Ministry of Agriculture, Nature and Food Quality (Plantenziektenkundige Dienst, Wageningen). Meanwhile I applied for a NWO-WOTRO scholarship for a PhD project, in collaboration with Utrecht University. In 2004 I started on this project, which has resulted in the publication of this thesis.



Photosynthesis measurements

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