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Dynamics and sustainable use of species-rich moist forests

A process-based modelling approach

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DYNAMICS AND SUSTAINABLE USE OF SPECIES-RICH MOIST FORESTS

A process-based modelling approach

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“The prerequisite for our survival and for peace among humankind is compliance with the many tolerance limits of the geo-biosphere’s dynamic stabilization, of the limits of robustness of our natural foundations of life and their regeneration cycles.”

Potsdam Manifesto 2005 “We have to learn to think in a new way”

ABSTRACT

Sustainable use of species-rich moist forests is hampered by an insufficient understanding of their dynamics and long-term response to different wood harvesting strategies. This thesis contributes to a better understanding of natural forest dynamics, explores the productivity of native forests subjected to different management strategies, and quantifies the ecological impacts of these strategies. The thesis focuses on two study regions: tropical montane cloud forest (TMCF) in central Veracruz, Mexico, and Valdivian temperate rain forest (VTRF) in northern Chiloé Island, Chile. The process-based forest growth model FORMIND is applied to study natural forest succession, to assess long-term ecological implications of fuelwood extraction on TMCF, to explore the potential of secondary TMCF for provision of ecosystem services and fuelwood, and to compare potential harvesting strategies for VTRF regarding forest productivity and ecological consequences.

Simulation results show that both forest types have a high potential for wood production. As wood extraction increases, the forest structure becomes simplified because large old trees disappear from the forest. The species composition shifts to tree species that are favoured by the respective harvesting strategy. The overall ecological impact increases linearly with the amount of extracted wood. Simulation results allow to define management strategies that balance conservation and production objectives, promote the regeneration of desired tree species, or minimise shifts in the species composition of the forest. Process-based forest models enhance our understanding of the dynamics of species-rich moist forests and are indispensable tools to assess long-term implications of anthropogenic disturbances on forest ecosystems. Thereby they contribute to the conservation and sustainable use of native forests outside protected areas.

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Introduction

1

Relevance

1.1

After massive deforestation and forest fragmentation in many regions of the world, conservation, sustainable management and even restoration of native forests have become a goal for numerous governmental and non-governmental organisations. Against this background, the EU project BIOCORES, in the framework of which the research for this thesis took place, has brought together scientists from Latin America and Europe to foster our understanding of forest ecology and deepen the theoretical foundations for “Biodiversity conservation, restoration and sustainable use in fragmented forest landscapes” (BIOCORES 2006). The project focused on tropical montane cloud forests (TMCF) in Mexico and Valdivian temperate rain forests (VTRF) in Chile, together with other Chilean temperate forests. These forest types have traditionally received less scientific and public attention than tropical lowland rain forests, yet they provide important ecosystem goods and services on a global, regional, and local scale. On a global scale, both study regions are recognised for their outstanding biodiversity in terms of species richness and/or the level of species endemism. They belong to the 25 biodiversity hotspots identified by Myers et al. (2000), based on vertebrate and vascular plant species richness, endemism, and degree of habitat loss, and VTRF has been classified among the 200 biologically most valuable and critically endangered ecoregions of the world (Olson and Dinerstein 1998). They are involved in climate regulation and carbon cycles (e.g. Dixon et al. 1994, Pregitzer and Euskirchen 2004, Snyder et al. 2004). On a regional scale, TMCF has an important function in the hydrological cycle by capturing water from the clouds and by storing water which is slowly released during the dry season. This way floods are prevented and a continuous dry-season runoff to downstream regions is assured (cf. Bruijnzeel 2004). VTRF plays a relevant role in erosion protection in a region with very high levels of rainfall. It assures high water quality of rivers, lakes, and coastal waters that is crucial for salmon breeding, which is one of the main export industries of Chile (Lara et al. 2003). On a local scale, both forest types serve as sources of fuelwood and timber for local market supply and offer a variety of non-timber forest products.

Apart from total protection within national parks or reserves, an ecologically appropriate management of forests can contribute to the conservation of native biodiversity and ecosystem services (e.g. Lindenmayer and Franklin 2002, Fredericksen and Putz 2003). To determine which types of management are appropriate and sustainable, information on long-term forest dynamics under different disturbance or management regimes is required. Such an understanding of long-term forest dynamics is often insufficient due to the long time scales of forest development and the lack of long-term experience with forest management. Even the global standards for certification of sustainable forest management defined by the Forest Stewardship Council (FSC 2004) only demand a "rationale for rate of annual harvest and species selection" because quantitative tools for the determination of sustainable cutting limits or the estimation of ecological consequences of different management options are largely unavailable.

1.2 Aims

This thesis aims to contribute to an ecologically appropriate use of species-rich moist forests by addressing three **general objectives**: to gain a better understanding of natural forest dynamics, to explore the productivity of the native forests under different management scenarios, and to quantify ecological impacts of these anthropogenic disturbances. The specific objectives reflect the different socio-economic context in the two study regions.

In central Veracruz, Mexico, land use is highly diverse and fragmented. Agricultural fields, pastures, and shade-coffee plantations are intermingled with old-growth TMCF forest fragments and secondary forests that are regrowing after abandonment of previous land uses (Williams-Linera et al. 2002). Until now, most fuelwood consumed for cooking and heating in the region comes from the old-growth TMCF fragments, where individual people regularly cut large living trees for their own needs or supply of local markets. This type of wood extraction has a long tradition. However, it is unclear, what ecological consequences it has for forest structure and composition in the long-term. In view of recent population growth and deforestation it is also unknown whether current levels of wood extraction are sustainable. The area of secondary forests in central Veracruz is increasing (Manson et al. unpubl. manuscript), and they play an increasingly important role in providing ecosystem services such as biodiversity conservation, water capture from clouds, and soil protection. Additionally, intensive management of young secondary forests for timber and fuelwood could provide an alternative to relieve pressure on the few remaining old-growth TMCF fragments. Hence, the **specific objectives** regarding **TMCF in central Veracruz, Mexico**, are to simulate natural forest succession, to investigate long-term impacts of repeated low-intensity selective logging on forest structure and composition as well as to evaluate the potential of secondary forests to provide ecosystem services and fuelwood.

The case of VTRF in southern Chile is different. Its dynamics are not very well known yet. The forests on the study site are apparently not in equilibrium, as there is no regeneration of the relatively shade-intolerant *Eucryphia cordifolia* which is present almost exclusively as large old individuals. Furthermore, the pristine native forests are severely threatened by conversion to pure plantations of exotic species, because there is little experience with their management, and because they are considered to be too complex to be managed. Therefore, the **specific objectives** regarding **VTRF in southern Chile** are to study long-term forest dynamics under different disturbance regimes as well as to show that the native forests have a silvicultural potential and to explore different management strategies as regards their productivity and ecological impacts.

Approach 1.3

There are two potential approaches to address the raised questions. First, one could design and conduct experiments combined with long-term monitoring of forest response to different silvicultural treatments. However, the design, execution and monitoring of large silvicultural experiments are costly and operationally difficult. Thus, modelling approaches which are complementary to experimental studies are needed to assess the long-term consequences of different management options and to provide guidelines for forest managers and planners aiming at reconciling conservation and production objectives (e.g. Lindenmayer and Franklin 2002).

There is a variety of forest models that simulate the dynamics of mixed forests. They differ in their basic unit (e.g. tree, size class, stand), consideration of spatial aspects, purpose of application (e.g. prediction of growth and yield vs. understanding of forest dynamics) etc. (see e.g. Shugart 1984, Vanclay 1995, Liu and Ashton 1995, Bugmann 2001, Porté and Bartelink 2002 for reviews). The majority of these models relies on long-term data from permanent sample plots from which statistical relations for recruitment, tree growth, and mortality are derived. Thus, model application is restricted to the conditions and management regimes for which data are available. Moreover, it is an exception that such data exist for forests that have not been subject to planned management and/or research for a long period of time. Additionally, the greater part of these forest models focuses either on the understanding of interactions between species with different ecological characteristics or on the prediction of expected forest growth and yield (e.g. Liu and Ashton 1995, Porté and Bartelink 2002). The simulation of management scenarios for species-rich forests needs to achieve both: on the one hand it must simulate species-specific responses to anthropogenic disturbance correctly, and on the other hand it must provide reliable information about wood volume increment under different management scenarios.

Thus, a model whose purpose it is to study the dynamics and to simulate management scenarios of species-rich, poorly studied rain forests needs to comply with several criteria. It needs to represent all important tree species or species groups present in the forest as well as to allow for a detailed incorporation of management scenarios, targeting only subsets of the tree species or preferred tree sizes. Furthermore, it needs to be applicable (in the sense of being feasible to be parameterised) to forests for which no long-term data on forest dynamics under different types of management are available.

The individual-oriented forest model FORMIND (e.g. Köhler and Huth 1998, Köhler 2000) complies with these requirements. It calculates the carbon balance for each individual tree on the basis of the light environment in the forest. Thus, the parameterisation effort is shifted from the phenological basis of realised tree growth to the physiological processes of photosynthesis and respiration. This way, the model explicitly simulates the outcome of the main process driving the dynamics of moist forests, namely the competition for light among different species, and forest response to different disturbance regimes can be derived from knowledge of physiological processes.

FORMIND has been developed in the late 1990s at the Center for Environmental Systems Research of the University of Kassel. It belongs to a family of rain forest models, out of which it is the only individual-oriented representative. Its relatively easy parameterisation has allowed a successful application to tropical lowland rain forest in several regions of the world, and made it the most widely applied model of species-rich tropical forests. It has been used to study forest dynamics and effects of logging, fragmentation, and climate change in Malaysia (Köhler et al. 2001, Köhler and Huth 2004, Huth et al. 2004, 2005), sustainable timber harvesting in Venezuela and Paraguay (Kammesheidt et al. 2001, 2002), and fragmentation effects in French Guyana (Köhler et al. 2003).

In the framework of this thesis, FORMIND has been parameterised for the first time for tropical montane forest (TMCF in Mexico) and temperate rain forest (VTRF in Chile). It also has been adapted to fit the specific requirements in the two study regions by implementing new logging strategies and including medium-sized natural disturbances which occur in southern Chile.

It is the first time for both forest types that a forest model is being applied in order to investigate long-term forest dynamics and ecological impacts of different management scenarios. Simulation results enhance our understanding of the dynamics of species-rich moist forests and contribute to the conservation and use of native biodiversity outside protected areas by providing guidelines for sustainable management and highlighting the potential of the forests for provision of ecosystem services (Franklin 1993, Armesto et al. 1998).

1.4 Structure of the thesis

This thesis is composed of eight chapters. After this general introduction, the **second** chapter presents the two study regions with their respective forest types, and places the research questions in the context of current and past land use patterns. The **third** chapter gives an introduction to the forest model FORMIND with a focus on changes made within the framework of this thesis.

The following four chapters deal with model applications to the study regions and represent the core of the thesis. These chapters are designed as research articles and can be read independently of each other. They have partly been submitted to scientific journals or are intended to be so. Chapters 4 – 6 refer to TMCF in Mexico whereas chapter 7 deals with VTRF in Chile. The **fourth** chapter presents the model parameterisation for TMCF in central Veracruz, Mexico. The ability of the model to reproduce observed forest characteristics is evaluated by comparing simulation results with available field data. Then the model is applied to simulate the course of forest regeneration after abandonment of previous land use. The **fifth** chapter investigates the long-term impact of repeated low-intensity selective tree harvesting for fuelwood on TMCF in central Veracruz. This type of human intervention is locally called “tala hormiga”, literally translated as “ant extraction”, and represents the main form of disturbance of remaining old-growth TMCF fragments. As knowledge of current use patterns is scarce, a wide range of potential

scenarios is compared regarding their long-term consequences for forest structure and composition. The **sixth** chapter studies the potential of young secondary TMCF forest stands to provide ecosystem services such as water capture from clouds and soil protection, and to be intensively managed for fuelwood production. This chapter also contains a validation of the model with field data from a chronosequence approach which became available towards the end of the work on this thesis (Muñiz-Castro et al. in press). The **seventh** chapter is dedicated to Chilean VTRF. It presents the model parameterisation as well as simulation results about long-term forest dynamics. Furthermore, three management strategies are evaluated in regard to their potential for wood production and ecological impacts. Results of an extensive sensitivity analysis of FORMIND can be 5
found in the Appendix of chapter 7.

The **eighth** chapter completes the thesis with a synthesising discussion of findings from the previous four chapters with respect to forest dynamics and sustainable use, a critical evaluation of the modelling approach, and an outlook to potential directions of further research. The **Appendix** contains a detailed description of FORMIND.

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THE STUDY AREAS 2

Tropical montane cloud forest in central Veracruz, Mexico 2.1

Introduction to tropical montane cloud forests 2.1.1

The potential global extension of tropical montane cloud forests (TMCF) is about 380,000 km². This area corresponds to only 2.5% of the potential area of tropical forests and 12% of tropical mountain forests (Bubb et al. 2004). Cloud forests are characterised by frequent cloud incidence, which is accompanied by reduced solar radiation and suppressed evapotranspiration. Cloud water is directly intercepted by the tree crowns ('horizontal precipitation' or cloud stripping) and added to the hydrological budget of the ecosystem (Hamilton et al. 1995). Worldwide, cloud forests can be found from as low as 500 m on oceanic islands up to 3500 m on large inland mountain systems. TMCF occurs within a wide range of rainfall regimes (500 – 10,000 mm per year). In general, cloud forests belong to the least studied tropical vegetation types and still little is known about their hydrological functioning and other ecosystem processes such as nutrient cycling (Hamilton et al. 1995, Bruijnzeel 2001, Williams-Linera 2002). They are threatened by conversion to agricultural and grazing land, fire, wood harvesting, alien species, and climate change, and currently seem to disappear at higher rates than tropical lowland rain forests (Bruijnzeel and Hamilton 2000, Bubb et al. 2004).

Despite the high variability of cloud forests, Hamilton et al. (1995) gave a working definition of TMCF. They identified a number of characteristics that are common to most cloud forests:

- TMCF occurs in a narrow altitudinal zone where persistent and frequent clouds cover the vegetation at a low height.
- The trees of TMCF are lower compared to tropical lowland rain forests and stem density is higher. The trees often exhibit a gnarled stature and have small, thick leaves.
- TMCF is characterised by a high abundance of epiphytes and low abundance of woody climbers.
- The proportion of endemic species is generally high in TMCF because of their fragmented and isolated nature.
- TMCF soils are often waterlogged and highly organic.

2.1.2 Abiotic conditions and forest characteristics

The Mexican state Veracruz extends along the Gulf of Mexico. The capital Xalapa is situated in the centre of the state at an altitude of 1500 m on the Neovolcanic Mountain Range that rises from the lowlands at the Gulf of Mexico to the central Mexican Highland. Xalapa is the eastern limit of TMCF distribution and is situated within the study area of this thesis. TMCF in central Veracruz – also referred to as "bosque mesófilo de montaña" (Rzedowski 1978) – occurs between 1200 and 2000 m a.s.l. In this paragraph it is analysed to what extend it complies with the above mentioned criteria.

Climate and hydrology – In the middle of the 19th century, Carl Christian Sartorius, a German immigrant in Mexico, noted about the climate in the region of Xalapa: 8

> "*A soft and gentle atmosphere prevails the whole year; it is pleasant during the day thanks to the breeze that comes from the sea, and fresh during the night due to the cold air that descends from the mountains. Here, the clouds carried by the trade winds towards the mountainous regions let all their humid load fall; the land never lacks fertilizing rain and the plants are refreshed by the moist nocturnal air.*" (Sartorius 1990, p. 67)*

Wet air coming from the Gulf of Mexico condensates and forms a persistent cloud layer during most of the year. During the dry-cool season from November to March the clouds are accompanied by fog at the vegetation level approximately every third day. The number of foggy days decreases to a few every month in the dry-warm season from April to May and the wet-warm season from June to October (Williams-Linera and Herrera 2003). Annual rainfall ranges from 1350 to 2200 mm and mean annual temperature from 12 to 18°C (Williams-Linera 2002). No data are available about the contribution of cloud stripping to the water budget, but the recent reduction of dry-season runoff to downstream regions has been attributed to the deforestation of uphill TMCF.

Vegetation – The English traveller William Bullock was impressed by the lush cloud forest vegetation:

> "*In a short ride we passed* […] *through deep sombre woods, composed of the noblest and most picturesque trees – lofty pines and oaks, with the tree that produces the liquid amber, and the elegant fern tree, with its waving, light, featherly branches (nine or ten feet long), formed conspicuous part.*" (Bullock 1824, p. 457)

In contrast to the above definition, trees in TMCF in central Veracruz are large, have a straight stature and broad thin leaves as they are typical for lower montane rain forests (Williams-Linera 2000, Bruijnzeel 2001). Three height layers can be distinguished. Emergent trees of sweet gum (*Liquidambar styraciflua*), oaks (*Quercus germana*, *Q. insignis*, *Q. sartorii*), and *Clethra mexicana* reach up to 35 m. The main canopy layer at 20 – 25 m is formed by other oak species (*Q. leiophylla*, *Q. salicifolia*, *Q. xalapensis*), *Beilschmiedia mexicana*, and *Magnolia schiedeana* amongst others. The understorey, below 15 m, is dominated by *Cinnamomum* spp., *Eugenia* spp., *Miconia* spp., *Palicourea* spp., *Turpinia insignis*, and several

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* These quotations are my personal translations of a Spanish translation of the original German book: C. C. Sartorius. 1855. Mexico. Landschaftsbilder und Skizzen aus dem Volksleben. Lange, Darmstadt, Germany.

species of tree ferns and palms. Most species that reach the main canopy have their origin in temperate regions and drop their leaves during several weeks between September and March, whereas the understorey of the forest is dominated by species with tropical affinity that are truly evergreen (Williams-Linera and Tolome 1996).

Epiphytes – Epiphytes (plants that live on host trees without deriving nutrients from them) are the most diverse group of TMCF flora (Challenger 1998). Mosses, lichens, ferns, bromeliads, and orchids almost entirely cover the branches of large old trees and give the forest its exuberant and mystical appearance (Fig. 2.1). In Mexico, TMCF is the vegetation type that harbours the highest number of epiphyte species, and the number of epiphyte species in central Veracruz is estimated to be at least 230 (Flores-Palacios 2003).

> *"Every tree is converted into a colony of innumerable plants; from the roots where the fungi and broomrapes are germinating, to the trunk, where every small crevice in the bark, every minuscule crack, is refuge of an orchid* [?] *or a cryptogam. In the ramifications of the trees you find large bromeliads that accumulate considerable amounts of water in the veins of their leaves to resist the dry periods. The branches are densely covered with tillandsias* [?] *of narrow and juicy leaves, and between them are dense bunches of blossoms hanging, the inflorescences of 'estanopias' and other species; like this everything appears, up to the crowns of the trees, often crowned by the northern 'misletos' and the tropical mistletoe of brilliant buds."* (Sartorius 1990, p. 68)

Species diversity and endemism – No other vegetation type in Mexico is more diverse per unit area than TMCF. TMCF covers < 1% of the territory of the state but contributes 10% of total plant diversity (SARH 1992, Williams-Linera 2002). Rzedowski (1992a,b) estimates that TMCF contains 3000 species of phanerogams, 30% of which are endemic to Mexico. Almost 300 species of amphibians, reptiles, birds, and mammals occur in TMCF, nearly half of which are endemic to Mexico (Flores-Villela and Gerez 1994). In central Veracruz, 64 tree species were found in 0.7 ha of TMCF (Williams-Linera 2002).

> "[…] *the hills are* […] *clothed with trees, shrubs and flowers, in such endless variety, that no part of Europe can vie with it."* (Bullock 1924, p. 457)

Topography and soils – The study area is situated on the lower eastern slopes of the volcano Cofre de Perote. The terrain is hilly to mountainous and slopes range from 0 to 30% (Williams-Linera et al. 2002). Soils derive from volcanic ashes and are classified as humic andosols (Rossignol 1987). They are deep, porous, susceptible to erosion by water, and their fertility is limited by low levels of phosphorus (Rossignol 1987). Soils contain a high amount of organic matter but are not waterlogged (Williams-Linera and Tolome 1996).

> *"In the woody region, the mountains are very eroded, narrow valleys, steep slopes and sometimes, coloured clay appears on the surface; sometimes decomposed lava and ashes. Everywhere signs of ancient volcanic activity are visible, deep craters, lava flows, elevated and, in certain locations, collapsed* [?] *mountains."* (Sartorius 1990, p. 70)

In summary, TMCF in central Veracruz could be called a seasonal cloud forest because fog or cloud cover at vegetation height is mostly confined to the dry season. During the wet season, most days are cloudy but the cloud base is well above the vegetation. Thus, the trees can grow fast and tall with straight trunks as they are characteristic for

Figure 2.1 Tree trunk covered with epiphytes in tropical montane cloud forest in central Veracruz, Mexico. Photo taken by G. Williams-Linera.

Figure 2.2 Pack animals are used to transport the fuelwood that was cut into pieces inside the forest to nearby villages. Photo taken by I. Haeckel.

lower montane rain forests (Bruijnzeel 2001). In terms of epiphyte abundance and occurrence of endemic species, however, TMCF in central Veracruz complies with the general definition given by Hamilton et al. (1995).

Land use 2.1.3

Before the Spanish Conquest in 1519, Totonacs and Nahua lived in the surroundings of Xalapa who preferred the lower parts of the region for subsistence cultivation of maize, beans, and chili (Marchal and Palma 1985). During the 17th century, the Spaniards concentrated the indigenous people in villages to be able to establish large land holdings (haciendas) where sugar cane was cultivated and cattle were raised. Successively, during the 18th century, the indigenous people were forced to move their villages towards higher altitudes (i.e. into the cloud forests) where they continued to cultivate maize, beans, chili, and squash in shifting cultivation. However, around 1850 Sartorius was astonished about the small proportion of cultivated land:

> *"When we crossed these fertile districts, in which you find large settlements, for example in the surroundings of Córdoba, Huatusco, Jalapa, Papantla, and other villages and hamlets, we were surprised to see so few cultivated plots, in relation to the large extensions of uninhabited solitudes. This is partly due to the scattered population and partly to the productivity of the soil, which, in a reduced space, offers huge quantities of nutritive fruits."*
>
> (Sartorius 1990, p. 69)

In the 19th century, coffee was introduced to the region as a major commercial crop, and by the end of the century sugar cane was replaced as the dominant crop by coffee plantations and cattle ranching. Often, the haciendas conserved a part of their land as forest reserve to assure the provision of water, wood, and fodder. The beginning of the 20th century brought a boom of coffee cultivation and the Mexican Revolution from 1910 to 1917. As a consequence, some of the large land owners were expropriated and 'ejidos', a special Mexican form of land tenure, were created. In ejidos, the land is communally owned but mostly individually cultivated.

Today, about 40 % of the land in the region Xalapa-Coatepec is ejido property and most farmers have the right to use 5 – 10 ha (Marchal and Palma 1985). The remaining land is mostly privately owned. The size of private properties spans a large range from < 1 ha to several hundred ha. Predominant land uses continue to be cattle ranching (37% of the area) and shade-coffee plantations (Williams-Linera et al. 2002). Minor land uses are cultivation of maize, potatoes, or Macadamia nut plantations. In the region west of Xalapa which was once entirely covered by cloud forests, only 10 % of the original forest remains in a relatively undisturbed state (Williams-Linera et al. 2002). Disturbed forests, secondary vegetation, and shade-coffee plantations cover 17% of the land. Secondary vegetation results from abandonment of other land uses such as agricultural fields or pastures.

Many forest fragments classified as undisturbed are in reality impacted by tree felling for fuelwood by the people who live around the forests (Fig. 2.2). Wood extraction is largely uncontrolled and not regulated by official management plans. However, a few ejidos in the region actively manage their forests to supply timber and fuelwood to regional markets. Apart from timber and fuelwood, non-timber forest products such as mushrooms and ornamental plants are harvested and small mammals are hunted.

In the future, the pressure on remaining TMCF fragments might further increase due to the overexploitation of adjacent pine-oak forests, which were traditionally preferred for wood extraction, because they contain more species with higher commercial value (Challenger 1998). Additionally, continuing population growth could increase fuelwood needs in the rural areas. Therefore, strategies for sustainable forest management are needed that reconcile economic interests of the land owners and the conservation of the ecosystem services the forests provide (e.g. water capture from clouds, soil protection, habitat for biodiversity). With the recently established system of payments for environmental services, Veracruz is one of the first Mexican states that give incentives to land owners to preserve their forests. Secondary forests are expected to increase in economic as well as environmental importance. They already cover almost the same area as primary forests, and have a high potential for the provision of ecosystem services as well as timber and fuelwood. Rational management of secondary forests could alleviate the pressure on primary forest.

2.2 Valdivian temperate rain forest in northern Chiloé Island, Chile

2.2.1 Introduction to temperate rain forests in southern South America

Temperate rain forests occur in coastal regions in the temperate climate zone of both hemispheres, e.g. in Canada, USA, Norway, Japan, Australia, New Zealand, Chile, and Argentine. They are characterised by growth limitation during the cold season – although the trees do not necessarily stop to grow – and sufficient water supply during the whole year (Armesto et al. 1999a). These forests cover only small areas and the temperate rain forests of southern Chile and Argentine constitute the second largest area of continuous temperate rain forests after the Pacific rain forests of western North America.

In Chile, temperate rain forests occur from south-central Chile (39° S) to Tierra del Fuego (55° S) (Arroyo et al. 1999). In the north, they are bordered by Mediterranean forests, in the east by montane vegetation of the Andes, and in the south and west by the Pacific Ocean. The cold Humboldt stream causes high air humidity along the Chilean coast with frequent fog (Arroyo et al. 1999). From north to south, mean annual temperatures decrease from 12° C to 5° C and annual rainfall varies between 1500 mm and more than 4000 mm. Annual variations in temperatures are very low (Arroyo et al. 1999). This climatic heterogeneity is reflected by a high variability of vegetation types.

Three broad vegetation types are distinguished among the Chilean temperate rain forests: Valdivian, North Patagonian, and Magallanic rain forest (e.g. Oberdorfer 1960). At a coarse scale, they replace each other from north to south or from lower altitudes to higher altitudes on the coastal and Andean mountain ranges. The Valdivian rain forest occurs from 39° to 43° S and below 400 m (Armesto et al. 1999b, Arroyo et al. 1999). It is characterised by broadleaved species (e.g. *Eucryphia cordifolia*, *Aextoxicon punctatum*, *Laureliopsis philippiana*), largely the absence of *Nothofagus*, and a high abundance of epiphytes and climbers (Armesto et al. 1999b). The North Patagonian rain forest occurs from 42° to 47°S and is characterised by *Nothofagus* and conifers (e.g. *Podocarpus nubigena*, *Saxegothaea conspicua*). Additionally, there are tree species that are common to both forest types, such as *Drimys winteri* and several myrtaceous species (Armesto et al. 1999b). The Magallanic rain forest is the southernmost forest type. It is formed by only two deciduous *Nothofagus* species (*N. pumilio*, *N. antarctica*).

The temperate forests of southern South America are predominantly evergreen and exhibit an exceptionally high productivity and high levels of biomass accumulation (more than 1000 t/ha) and high density (up to 10,000 stems/ha, > 5 cm diameter at breast height) (Armesto et al. 1999a). They harbour an unusual diversity and abundance of epiphytes and climbers which are normally rare or uncommon in temperate forests (Armesto et al. 1999a). Additionally, they are characterised by high levels of endemism, because of their long isolation from any other forests. During the Tertiary they originated on the supercontinent Gondwana which at that time connected South America, Antarctica, Australia and New Zealand (Armesto et al. 1999a). Because of the shared origin, the forests of those regions have many taxa in common that are absent from northern continents, e.g. *Nothofagus* and *Eucryphia*. Other genera are endemic to southern South America, such as *Aextoxicon*, *Amomyrtus*, *Laureliopsis*, and *Luma*. Today, the forests of southern Chile and Argentine are separated from the nearest forests in northeast Argentine and southeast Brazil by more than 2000 km and insuperable barriers such as the Andean range and the Patagonian grassland (Armesto et al. 1999a).

2.2.2 Abiotic conditions and forest characteristics

The second study area of this thesis is located on the northern coast of Chiloé Island. On his voyage with the Beagle, Charles Darwin visited the island in 1834 and 1835, and described it very vividly:

> *"The island is about 90 miles long, with a breadth of rather less than 30. The land is hilly, but not mountainous, and is every where covered by one great forest, excepting a few scattered green patches, which have been cleared round the thatched cottages. From a distance the view somewhat resembles Tierra del Fuego; but the woods, when seen nearer, are incomparably more beautiful. Many kinds of fine evergreen trees, and plants with a tropical character, here take the place of the gloomy beech of the southern shores. In winter the climate is detestable, and in summer it is only a little better. I should think there are a few parts of the world, within the temperate regions, where so much rain falls. The winds are very boisterous, and the sky almost always clouded: to have a week of fine weather is somewhat wonderful."*
>
> (Darwin 1989, p. 218)

Climate and topography – Still today the climate on Chiloé Island is very wet and temperate (Luebert and Pliscoff 2005). Rainfall occurs throughout the year with an annual average of more than 2400 mm. Mean annual temperature is 10.7°C with a monthly maximum of 13.8°C in January and a minimum of 8.3°C in July. In winter, strong northerly winds ("temporales") occur that uproot trees and damage houses. The study area is situated about 100 m above sea level. The terrain is hilly and steep slopes fall to

Figure 2.3 Flowering emergent *Eucryphia cordifolia* trees in the study area in Guabún, northern Chiloé Island, Chile. Photo taken by I. Díaz.

Figure 2.4 Plantation of Monterrey pine (*Pinus radiata*) surrounded by old-growth Valdivian rain forest near Valdivia, Chile. Photo taken by J. Armesto.

the sea. Soils are relatively shallow and have developed on plio-pleistocenic volcanic rocks (Mardones 2005). Information on nutrient content of the soils is not available (M. Carmona, pers. comm.).

Vegetation – The arboreous vegetation of coastal VTRF comprises about 15 tree species, such as ulmo (*Eucryphia cordifolia*), tepa (*Laureliopsis philippiana*), olivillo (*Aextoxicon punctatum*), canelo (*Drimys winteri*) and several species of the Myrtaceae family (*Amomyrtus meli*, *Amomyrtus luma*, *Myrceugenia planipes*, *Myrceugenia ovata*, *Luma apiculata*) (Armesto et al. 1999b). Mature forest stands are characterised by old, emergent *E. cordifolia* trees that grow up to 40 m high (Fig. 2.3). The main canopy is dominated by *L. phillipiana* and *A. punctatum* which reach a maximum height of 30 – 35 m. In terms of stem numbers, the myrtaceous species dominate. They usually reach their maximum size at a height of 15 – 20 m. In mature forests, regeneration of the relatively shade-intolerant *E. cordifolia* is rare, and *E. cordifolia* may completely disappear, leaving a forest of exclusively shade-tolerant species (e.g. Donoso et al. 1984, 1985, Veblen 1985). In forest stands where frequent disturbances occur, the bamboo species quila (*Chusquea quila*) dominates the understorey in canopy gaps. Secondary forests are characterised by shade-intolerant shrubs (e.g. *Embothrium coccineum*, *Ovidia pillo-pillo*), *E. cordifolia*, *D. winteri*, and myrtaceous species.

Fauna – VTRF on Chiloé Island harbours a variety of mammal and bird species, many of which are endemic to temperate forests of southern South America. Examples include Dawin's Fox (*Pseudalopex fulvipes*), which is endemic to Chiloé Island and the Cordillera de Nahuelbuta, the pudu (*Pudu puda*), the world's smallest dear, the guiña (*Oncifelis guigna*), a wild cat, and the "monito del monte" (*Dromiciops gliroides*), phylogenetically the oldest living marsupial (Jiménez 2005a,b,c). Of the 44 bird species reported for Chilean temperate rain forests, 29 are endemic to southern South America and 14 to the temperate rain forests of Chile and Argentine (Rozzi et al. 1996). Mutualistic plant-animal interactions play an exceptionally important role in pollination and seed dispersal in VTRF (Armesto et al. 1999a). Insect pollination (77% of plant species) dominates over hummingbird (13%) and wind (10%) pollination (J. Armesto, unpubl. review). More than 60% of plants of the forests in Chiloé Island have fleshy fruits (Armesto and Rozzi 1989) which indicates the importance of seed dispersal by animals.

2.2.3 Land use

The first humans arrived in the forested regions of Chile about 11,000 years ago (Mooney 1977). They used fire to clear the forest for agricultural activities and extracted fuel wood. But only with the Spanish Conquest in the 16th century, humans began to exert major impacts on the forests. Huge areas were burnt to clear land for agriculture and pasture for introduced cattle (Donoso and Lara 1999). Valuable timber species were selectively logged. On Chiloé Island, alerce (*Fitzroya cupressoides*) forests were cut, but other forest types in Chiloé remained little affected (Donoso and Lara 1999). In 1834/35, when Charles Darwin visited Chiloé, the forests of the island were still little fragmented by human activity:

> *"The forests are so impenetrable, that the land is nowhere cultivated except near the coast, and on the adjoining islets. [...] Although the fertile soil, resulting from the decomposition of volcanic rocks, supports a rank of vegetation, yet the climate is not favourable to any production which requires much sunshine to ripen it. There is very little pasture for the larger quadrupeds; and in consequence, the staple articles of food are pigs, potatoes and fish."*
>
> (Darwin 1989, p. 219)

The 19th century was characterised by increased deforestation. After the defeat of the indigenous Mapuche in the region north of Valdivia a wave of German settlers cleared large parts of this still mostly forested region (Donoso and Lara 1999). During the last decades of the 19th century, Monterrey pine (*Pinus radiata*) was introduced to Chile, and within 100 years succeeded to completely dominate Chilean wood production. In the 1930s, pine made up for 3% of wood production, compared to 97% from native species. However, in 1980, 85% of the wood production came from pine and only 15% from native species (Donoso and Lara 1999). Beginning in the 1970s, the state had given subsidies for the establishment of exotic tree plantations which in the following rapidly expanded at the expense of native forests (Fig. 2.4). This replacement of the native forests proceeded from north to south, and from more accessible to less accessible sites. As a consequence, Chiloé is now at the southern margin of the plantation frontier. During the last thirty years, 30% of the native forests of northern Chiloé and the opposite mainland were converted to shrubland (Echeverría 2005). Further deforestation and conversion to non-native tree plantations might happen in the near future.

Contrary to Darwin's experience, today the landscape in northern Chiloé is very fragmented. Land is mostly privately owned, and cattle and sheep pastures dominate. Moreover, people live from fishing, gathering of algae, and salmon culture. The native forests are selectively logged for healthy and large trees of species that produce high quality timber (e.g. *E. cordifolia*, *L. philippiana*, *P. nubigena*) (Donoso and Lara 1999). These practices leave "creamed" forests with reduced regeneration capacity. However, since the 1970s, the Universidad de Chile and the Universidad Austral de Chile started scientific projects to investigate the potential of silvicultural management of the native forests (Donoso and Lara 1999). Even if management of Chilean evergreen rain forests is considered to be difficult (Donoso 1989), a workshop that was held in 1989 in Valdivia concluded that native forests can be managed, that volume increments are high, and that their management could even be more profitable than that of exotic species taking into account the higher prices for timber from native species (Donoso and Lara 1999).

Recently, five main threats to rain forests in the Valdivian eco-region have been identified by Cavelier and Tecklin (2005). These are substitution of native forests by plantations of non-native tree species, forest exploitation for timber and wood chips, fuelwood extraction, fire, and overgrazing. Still, the establishment of plantations of exotic tree species is subsidised, plantation forestry is expanding southwards, and a new road is planned along the coast south of Valdivia that would open access to the largest remaining tracks of old-growth Valdivian rain forest on the mainland in Chile. Additionally, only about 20% of forest operations in native forests are supported by authorised management plans (Emanuelli 1996). These facts points to the opportunity to improve the management of native forests (Donoso and Lara 1999). During the last years, awareness of the importance of conservation and sustainable use of the unique forests and the ecosystem services they provide has risen (Armesto et al. 1998, Donoso and Lara 1999, Lara et al. 2003, Cavelier and Tecklin 2005) and numerous private and non-governmental organisations are involved in projects that promote forest and watershed conservation, environmental education, as well as sustainable use of the native forest resources (e.g. Agrupación de Ingenieros Forestales por el Bosque Nativo, Fundación Senda Darwin, The Nature Conservancy, World Wide Fund for Nature).

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The forest growth model FORMIND 2.3

3

General description[*] 3.1

This description follows the ODD protocol which has been proposed as a standard protocol for describing individual- and agent-based models (Grimm and Railsback 2005, Grimm et al. in press). A more detailed description of the mathematical formulation of ecological processes, and tables with model parameters for TMCF in central Veracruz, Mexico, and VTRF in northern Chiloé Island, Chile, can be found in Appendix A. The original model description of FORMIND 2.0 is given in Köhler (2000).

Purpose 3.1.1

The individual-oriented forest growth model FORMIND was developed to study the long-term response of uneven-aged mixed species rain forests to natural or anthropogenic disturbances (e.g. wind throw, logging, fragmentation).

State variables and scales 3.1.2

FORMIND is a three-dimensional, grid-based, individual-oriented model. It formulates the ecological processes on three hierarchical levels: tree cohorts, grid cells (below called patches) and hectares. To enable an individual-based simulation of the dynamics of species-rich forests, tree species that occur at the study sites are grouped into plant functional types (PFT) with similar shade tolerance and maximum attainable height. All trees that belong to the same PFT, and that establish in the same year in the same patch are grouped into a cohort. All trees in one cohort are equal in size. Trees with a diameter > 40 cm are usually simulated individually, because all other trees from their cohort have died. Each tree cohort is characterised by the state variables PFT, number of individuals, above-ground biomass of one individual and position (i.e. the patch where the cohort is located). From the biomass of the tree all other morphological variables of the tree such as diameter at breast height (dbh), height, crown diameter, crown depth, and stem volume are derived.

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[*] The model description can also be found in the online appendix of the publication Grimm et al. *In press*. A standard protocol for describing individual-based and agent-based models. Ecological Modelling.

A patch is characterised by the tree cohorts present in the patch, and its coordinates within the hectare where the patch is located. The size of a patch corresponds to the crown size of mature trees (here 20 m × 20 m). Leaf area of the trees is added up in small horizontal layers, and the available light is calculated for each layer. Neighbourhood relations link each patch to its four direct neighbours (across hectare boundaries) to allow dying trees to fall into another patch.

Finally, hectares are characterised by the patches they comprise, and they contain higher-level information on overall logging potential (i.e. the number and stem volume of harvestable trees) of all patches that belong to the hectare. Hectares are arranged spatially as a square, such that the simulation area necessarily is a square number of hectares. Minimum extent of the simulation area is one hectare, and several hundreds of hectares can be simulated. The simulation area is simulated as a torus (i.e. with periodic boundary conditions). The model simulates a forest in annual time steps and simulation runs usually comprise several hundred years.

3.1.3 Process overview and scheduling

It is assumed that light availability is the main driving force for individual tree growth and forest succession. Within each patch all trees compete for light and space following the gap model approach (Shugart 1998). The light climate in the forest interior of each patch is calculated via an extinction law depending on the vertical distribution of the leaf area of the trees (Monsi and Saeki 1953). Depending on the resulting light climate, the light availability is determined for every tree. Annual growth of each tree is calculated on the basis of the main physiological processes photosynthesis and respiration, and litter fall. Growth process equations are modified from the model FORMIX3-Q (Ditzer et al. 2000, Huth and Ditzer 2000). Allometric functions relate above-ground biomass, stem diameter, tree height, crown diameter, and stem volume. Tree mortality can occur either through self-thinning in dense patches, stochastic mortality, gap creation by large falling trees, or medium-scale wind throws. Recruitment occurs when the light intensity at forest floor exceeds a PFT-specific threshold. Recruitment rates describe the number of small trees growing over the dbh threshold of 1 cm per year.

The model proceeds in annual time steps. Within each year – or time step – six modules are processed in the following order: occurrence of medium-scale disturbances (only in the case of VTRF in northern Chiloé Island), recruitment, mortality, calculation of the light climate in the forest interior, growth, and logging. Disturbances act on the level of hectares; establishment, calculation of light climate, and logging are executed for each patch, whereas growth and mortality are determined for each tree cohort.

3.1.4 Design concepts

Emergence – Annual growth rates of trees are not directly built into the model but emerge from individual tree characteristics (photosynthetic capacity and respiration) and the competition for light between the trees in a patch due to shading. Recruitment rates depend on the light available at the forest floor, and mortality is composed of different processes. Hence, realised recruitment, growth, and mortality rates are characteristics that emerge from the current tree assemblage of a patch (i.e. number, size and PFT of trees in the patch). Furthermore, all characteristics at higher levels (population level, patch level, stand level) emerge from the fate of and interactions between individual trees.

Sensing – The current size of a tree affects both its potential biomass production (through the amount of leaf area) and its mortality rate which is elevated for small trees.

Interaction – Interaction between single trees of the same patch occurs via competition for light and space (self-thinning). Direct interactions between trees of different patches occur when dying large trees fall over and destroy a proportion of the trees in the patch where their crown hits the ground.

Stochasticity – All facets of mortality are described on the basis of probabilities. Mortality due to space competition affects randomly chosen trees. The observation that only some of the dying trees fall over and kill other trees is realised via a “falling probability”. In the case of VTRF in northern Chiloé Island, medium-scale disturbances affect a given hectare with a certain probability. Likewise, the number of disturbed patches per disturbance event is chosen randomly.

Collectives – All trees that belong to the same PFT, and that establish in the same year in the same patch are grouped into a cohort. All trees in one cohort are equal in size. Trees with a dbh > 40 cm are usually simulated individually, because all other trees from their cohort have died.

Observation – The individual-oriented approach allows to compare model outcomes with field observations on the individual-tree level, on the population level as well as on the level of the entire tree community. To test the model, we compare simulated and measured growth and mortality rates, as well as stem numbers and basal area for each PFT, or overall forest characteristics such as mean leaf area index (LAI) or size distributions. This wide range of possibilities to check the behaviour of the model ensures that the key processes are included and that the model is able to reproduce observed forest characteristics.

For an assessment and comparison of different logging scenarios we record several PFT-level and stand-level variables over time. These include stem numbers, basal area, biomass and stem volume of the different PFTs, stem numbers in different diameter classes, stand LAI, harvested stem volume, logging damages, and fraction of forest in gap, building or mature phase.

Initialisation 3.1.5

Every state of the forest, described in terms of stem number-diameter distributions for the different PFTs, can be used as initial situation for a model run. To study long-term forest dynamics after natural large-scale disturbance we start from a treeless area which is regarded to be suitable for establishment of all PFTs. For the logging scenarios we use inventory data of old-growth forest from the study site as initial situation. The inventory data are expanded to correspond to the simulation area and individual trees are randomly distributed among the different patches.

Input 3.1.6

Site conditions are assumed to be homogeneous and there is no inter-annual variability of environmental conditions.

3.2 Adaptations of FORMIND 2.3

3.2.1 Recruitment

A new simplified regeneration mode “ingrowth” was implemented. FORMIND2.2 recruitment routines “seedpool” and “seedtree” work with seed numbers, the seeds are stored in a seed pool and affected by subsequent seed mortality before they provide the basis for ingrowth into the seedling layer of trees with a dbh of 1 cm. Both routines can be combined.

In “ingrowth”, ingrowth rates (N_{max}) are directly used to determine the number of ingrowing seedlings. Additionally to minimum light intensity required for establishment of a given PFT (I_{min}), a maximum light intensity (I_{max}) was introduced, because in Chilean VTRF it was observed that certain species do not establish in open space or arrive later in large gaps than other species. Thus, if minimum and maximum light requirements for establishment of a given PFT are fulfilled, N_{max} small trees with a dbh of 1 cm establish.

3.2.2 Growth

The biomass production routine of FORMIND 2.2 was modified. In FORMIND 2.2, net biomass increment of a tree (B_{inc}) was calculated as

$$B_{inc} = PB \cdot GL \cdot (1 - 0.25) - MR\,,$$

where PB is gross biomass production, GL is growth limitation, and MR maintenance respiration. GL is a term that assures decreasing B_{inc} when a tree reaches its maximum diameter. The term -0,25 represents the fraction of biomass that is lost due to growth respiration, i.e. the respiration cost of the build-up of new biomass. In Ryan (1991) it was stated that for the build-up of 1 g C, on average 0.25 g C are invested by the plant. Thus, growth respiration has to be applied to the difference of gross biomass production and maintenance respiration, because this is the portion of gross biomass production that is available for build-up of new biomass. Additionally, growth limitation of biomass increment was abolished in FORMIND 2.3. The decrease of B_{inc} for large trees was assured by fitting the parameters for maintenance respiration which depends on the biomass of the tree. The resulting net biomass production formula of FORMIND 2.3 is

$$B_{inc} = (1 - 0.2) \cdot (PB - MR)\,.$$

Furthermore, respiration parameters were made specific for each PFT, in contrast to being specific for each light group (i.e. all PFTs with the same shade tolerance). Thus, now it is possible to fit maintenance respiration parameters in a way that available field data on diameter increment of the different PFTs are reproduced. Genetic algorithms were applied for the parameter fitting, and maximum diameter increment was used as fitting criterion.

Geometry 3.2.3

The data basis for Mexican TMCF and Chilean VTRF regarding tree geometry was less extensive than for former regions of model application. Thus, many allometric relationships were used in a simplified form. The relationship between stem diameter and crown diameter was assumed to be linear instead of nonlinear. Leaf area calculation was totally omitted. Instead, leaf area index (L_{max}) of a single tree was set to a fixed value. For species of Chilean VTRF, data on stem volume were available in the literature. To match those data, the form factor (f) was made species-specific, but was, in contrast to FORMIND 2.2, not a function of tree diameter.

25

Logging 3.2.4

Selective logging was made more flexible by introducing a new parameter indicating the maximum diameter of a tree allowed to be cut. Thus, now logging can be restricted to certain diameter ranges by defining minimum and maximum diameter thresholds.

Logging in bands was implemented which has been proposed as one potentially suitable logging strategy for VTRF in southern Chile. For logging in bands, each hectare is divided into five 20 m wide bands which are recurrently clear-cut. All trees from the logged band are removed, regardless of their PFT or dbh.

Natural disturbances 3.2.5

In southern Chile winterly storms (“temporales”) cause occasional wind throw events of a large number of trees that create larger gaps than the usual falling of one large tree. These medium-size disturbances were modelled by removing all trees in an area comprising 2 – 4 neighbouring patches, thus creating gaps of 800 – 1600 m². The probability that a certain hectare is affected by a wind throw is 0.8% per year. Disturbance size (i.e. 2, 3, or 4 patches) is drawn from a uniform distribution.

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Modelling the dynamics of tropical montane cloud forest in central Veracruz, Mexico*

Abstract

The area covered by tropical montane cloud forest (TMCF) in central Veracruz has decreased rapidly over the last 50 years. Deforestation has been accompanied by the fragmentation of the remaining forest. Restoring the TMCF and the important ecological services it provides (e.g. water capture, soil conservation) requires an understanding of the dynamics of this ecosystem. The objectives of this study are to investigate the dynamics of the fragments of old-growth forest and especially its regeneration after abandonment of other land uses. We apply a modified version of the process-based forest growth model FORMIND. FORMIND is individual-tree-oriented and simulates the spatio-temporal dynamics of an uneven-aged mixed forest stand. The modifications include (1) grouping tree species according to their light demands and maximum heights, (2) defining regeneration, growth and mortality parameters for each species group, and (3) developing allometric relations of tree geometry. We verify the model by comparing model outcomes and observed patterns (e.g. inventory data, diameter increment data). Results show that the model is able to reproduce the structure of old-growth forest. Simulations of forest regeneration reveal that aggregated variables (e.g. total stem number and total basal area) reach values of an old-growth forest after approximately 80 years, whereas the proportion of basal area of the different species groups continues to change until 300 years after the beginning of succession. The gained insights can support regional decision making in forest conservation and restoration planning.

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1 Introduction

Compared to temperate forests, forest modeling in the tropics faces several difficulties: the richness in tree species, lack of data on tree ages, and the lack of long-term data on forest structure. Nevertheless, in tropical lowland rain forest a variety of phenomena has successfully been studied with the help of forest models. Model applications include the investigation of impacts of alternative logging regimes on forest structure and timber yield in the long term, fragmentation and edge effects, etc. (e.g. Vanclay 1995, Chave 1999, Liu and Ashton 1999, Huth and Ditzer 2001, Köhler et al. 2003). Tropical montane 28 cloud forest (TMCF) poses similar problems and compared to tropical lowland rain forest there is even less knowledge and fewer data available for TMCF (e.g. Hamilton et al. 1995). Nevertheless, we believe that it can be useful to combine available knowledge in a simulation model to investigate questions that are not easily accessible for empirical research, such as the study of long-term phenomena like forest succession after disturbance or long-term impacts of selective logging on forest structure and composition.

As a starting point we focus on the TMCF of central Veracruz, Mexico. The area covered by TMCF in central Veracruz has decreased rapidly over the last 50 years (Williams-Linera et al. 2002). Deforestation has been accompanied by the fragmentation of the remaining forest. Restoring the TMCF and the important ecological services it provides (e.g. water capture, soil conservation) requires an understanding of the dynamics of this ecosystem. Remaining old-growth forest fragments have been studied during the last decade (e.g. Williams-Linera 1991, 1993, 1996, 2002, Williams-Linera et al. 2002, Álvarez-Aquino 2004, 2005). The collected data provide an initial basis for the modelling of cloud forest dynamics.

We aim to address questions related to forest regeneration and succession with the process-based simulation model FORMIND (Köhler and Huth 1998), which is based in parts on the more aggregated forest model FORMIX3 (Huth et al. 1998, Ditzer et al. 2000, Huth and Ditzer 2000, Kammesheidt et al. 2002, Glauner et al. 2003). The model is individual-tree-oriented and simulates the spatio-temporal dynamics of an uneven-aged mixed forest stand. Tree species are aggregated into plant functional types (Köhler et al. 2000). A former model version, FORMIND 2.0, was used to study the dynamics of disturbed forest in Malaysia, Venezuela, and French Guiana (Kammesheidt et al. 2001, Köhler et al. 2001, 2003, Köhler and Huth 2004, Huth et al. 2005).

In this paper, (1) we describe the main processes and principal assumptions of the forest growth model FORMIND, as well as its parameterisation for TMCF in central Veracruz, Mexico; (2) we test the ability of the model to reproduce structure and composition of TMCF in central Veracruz by comparing model results with inventory data and field observations; and (3) we predict regeneration time and progression of succession after large-scale disturbance (e.g. clear-cutting) or abandonment of previous land use.

Methods

4.2

Study sites

4.2.1

Five forest fragments in the TMCF region of central Veracruz, Mexico (19°30' N, 96°54' W) were selected for this study. The sites are located at an altitude between 1250 and 1875 m. The climate is mild and humid throughout the year with three seasons. A relatively dry-cool season extends from November to March, a dry-warm season from April to May, and a wet-warm season from June to October. Annual precipitation varies between 1350 and 2200 mm; mean annual temperature is between 12 and 18°C (Williams-Linera 2002). The soil has been classified as Andosol (Rossignol 1987). The number of observed trees species (> 5 cm dbh) varies between 16 and 28 in the study sites. Dominant tree species include *Carpinus caroliniana*, *Clethra mexicana*, *Fagus grandifolia*, *Liquidambar styraciflua*, *Quercus germana*, *Q. leiophylla*, *Q. xalapensis*, and *Turpinia insignis*.

Model description

4.2.2

Main processes – The individual-oriented forest growth model FORMIND2.3 simulates the spatial and temporal dynamics of uneven-aged mixed forest stands (Köhler and Huth 1998, Köhler 2000). The model simulates a forest (in annual time steps) of several hectares as a mosaic of interacting grid cells with a size of 20 m × 20 m, corresponding to the crown size of mature trees. It is assumed that light availability is the main driving force for individual tree growth and forest succession. Tree growth is not limited by water or nutrient shortage. Within the grid cells, trees are not distributed in a spatially explicit manner, and thus they all compete for light and space following the distance-independent gap model approach (Shugart 1998). For the explicit modelling of the competition for light each grid cell is divided into horizontal layers. In each height layer the leaf area is summed up and the light climate in the forest interior is calculated via an extinction law (Monsi and Saeki 1953). The carbon balance of each individual tree is modelled explicitly, including the main physiological processes (photosynthesis, respiration). Growth process equations are partly taken from the model FORMIX3-Q (Ditzer et al. 2000). Allometric functions relate above-ground biomass, stem diameter, tree height, crown diameter and stem volume. Tree mortality can occur either through self-thinning in dense grid cells, senescence, or gap formation by large falling trees. Gap formation links neighbouring grid cells. Regeneration rates are effective rates regarding the recruitment of small trees at a diameter at breast height (dbh) threshold of 1 cm, with seed loss through predation and other processes already being implicitly incorporated.

Species grouping – To enable an individual-based simulation of forest dynamics, the 58 native tree species that occur in the study sites have to be grouped into plant functional types (PFT). Criteria for classification into PFTs are light demand and maximum attainable height. Three levels of shade tolerance are distinguished (shade-intolerant (i), intermediate (m), and shade tolerant (t)). Three height groups are considered: small trees (≤ 15 m tall, ≤ 35 cm dbh), canopy trees (≤ 25 m tall, ≤ 80 cm dbh), and emergent trees (≤ 35 m tall, ≤ 100 cm dbh). This classification results in six PFTs because some of the combinations are rare (Table 4.1). A complete species list is given in Appendix B of the thesis.

Table 4.1 Definition of plant functional types (PFTs) according to shade tolerance (T) and maximum attainable height (H_{max}). Three levels of shade tolerance are distinguished: i = shade-intolerant, m = intermediate, t = shade-tolerant. The successional status refers to the stage of succession in which a PFT attains maximum basal area values.

Plant functional type	PFT	T	H_{max}	Examples
Early successional small trees	1	i	15 m	*Heliocarpus, Myrsine*
Mid successional small trees	2	m	15 m	*Miconia, Oreopanax*
Late successional small trees	3	t	15 m	*Cinnamomum, Ilex*
Mid successional canopy trees	4	m	25 m	some *Quercus* spp.
Late successional canopy trees	5	t	25 m	*Magnolia, Beilschmiedia*
Emergents	6	m	35 m	*Liquidambar, Clethra*

4.2.3 Model parameters

In the description of model parameters we focus on biologically relevant parameters, more technical details can be found in Köhler (2000).

Environmental parameters – The climate of central Veracruz is mild and humid, and we assume that trees can grow throughout the whole year. Mean annual light intensity above the canopy was estimated to be 600 μmol(photons)·$m^{-2}s^{-1}$. Hafkenscheid (2000) measured average values of 1150 μmol(photons)·$m^{-2}s^{-1}$ on a sunny day and 260 μmol(photons)·$m^{-2}s^{-1}$ on a totally overcast day in the Jamaican Blue Mountains. As annual average light intensity he calculated 650 μmol(photons)·$m^{-2}s^{-1}$. Measurements of the light extinction coefficient for TMCF are not available. In tall tropical lowland forests a commonly observed value is 0.7 (Kira 1978). Hafkenscheid (2000) estimated the light extinction coefficient for short-statured upper montane rain forest to be 0.5. Hence, a light extinction coefficient between 0.5 – 0.7 seems to be appropriate for TMCF. In the simulation model we use the value 0.5.

Parameters related to tree growth – Growth characteristics are assumed to be related to shade tolerance and apply for all PFTs with the same shade tolerance, except in the case of respiration, where parameters are unique to each PFT.

The rate of photosynthesis P is modeled as a saturating function of the irradiance (I_0) available at the crown of the tree,

$$P(I_0) = \frac{\alpha\, I_0\, p_{max}}{\alpha\, I_0 + p_{max}},$$

with p_{max} being the maximum rate of photosynthesis and α the initial slope of the light-response curve. In a Panamanian tropical lowland rain forest Ellis et al. (2000) measured p_{max} for some tree species (or species of the same genus) that also occur in the cloud forest of the study area: *Trema micrantha* (shade-intolerant, 18 μmol(CO_2)·$m^{-2}s^{-1}$), *Palicourea guianensis* (intermediate, 16 μmol(CO_2)·$m^{-2}s^{-1}$), *Zanthoxylum beliziense* (intermediate, 15 µmol(CO_2)·$m^{-2}s^{-1}$), *Beilschmiedia pendula* (shade-tolerant, 12 µmol(CO_2)·$m^{-2}s^{-1}$. Dillenburg et al. (1995) report the maximum photosynthetic rates of sun leaves of *Liquidambar styraciflua*, which is classified as an intermediate species, to be higher than 20 µmol(CO_2)·$m^{-2}s^{-1}$ at an irradiance of 2000 µmol(photons)·$m^{-2}s^{-1}$. In Colombian TMCF, Letts and Mulligan (this volume) measured p_{max} values between 4 and 11 µmol(photons)·$m^{-2}s^{-1}$. For the three light groups p_{max} is chosen to be 20 µmol(CO_2)·$m^{-2}s^{-1}$ for shade-intolerant PFTs, 16 µmol(CO_2)·$m^{-2}s^{-1}$ for intermediate, and 10 µmol(CO_2)·$m^{-2}s^{-1}$ for shade-tolerant PFTs (Fig. 4.1). The slope of the light-response curve α was assumed to be 0.15, 0.2 and 0.25 µmol(CO_2)·$m^{-2}s^{-1}$ for shade-intolerant, intermediate, and shade-tolerant PFTs, respectively. Self-shading of the canopy is accounted for using an approach of Thornley and Johnson (1990). The proportion of light transmitted by leaves was estimated to be 0.1 (Larcher 2001).

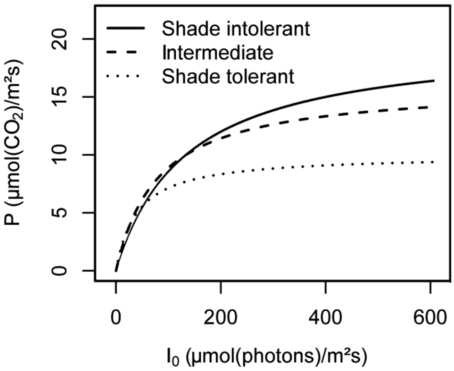

Figure 4.1

Relationship between irradiance (I_0) and photosynthetic production (P) for three levels of shade tolerance.

Respiration processes can be divided into growth respiration during the build-up of new biomass and maintenance respiration of living biomass. Growth respiration is estimated to amount to 25% of net production of the tree according to Ryan (1991). Maintenance respiration r is assumed to be exponentially dependent on the living biomass (B) of the tree,

$$r = r_0 \cdot B^{r_1}.$$

Parameters of the relationship are fitted such that the simulated diameter increment of each PFT matches the available diameter increment data. We simulate the growth of a single tree of each PFT under full sunlight conditions and compare its annual diameter increment to measured annual diameter increment of TMCF species from the Botanical Garden "Francisco Javier Clavijero" in Xalapa, Mexico, and TMCF fragments (Williams-Linera 1996). Simulated and observed diameter increment values are shown in Figure 4.2.

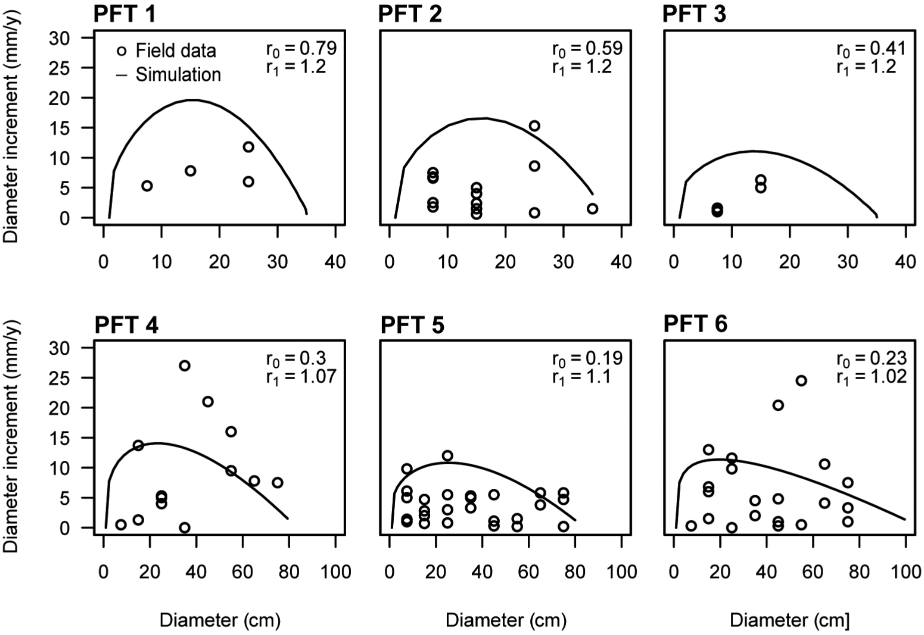

Figure 4.2 Measured and simulated annual diameter increment for the six plant functional types (PFT). Simulations were carried out under full light conditions (600 µmol(photons)·m^{-2}s^{-1}) and represent maximum potential growth. r_0 and r_1 are parameter values of the formula for maintenance respiration ($r = r_0 \cdot B^{r_1}$). Field measurements were taken in different light environments (Williams-Linera 1996).

For 26 species that occur in the TMCF of central Veracruz, or species of the same genus, stem wood densities are available (Bárcenas et al. 1998, Aguilar-Rodríguez et al. 2001). Wood densities of species with the same shade tolerance were averaged. Resulting arithmetic means are 0.55 g/cm³, 0.65 g/cm³ and 0.7 g/cm³ for shade-intolerant, intermediate, and shade-tolerant species, respectively. No marked differences between wood densities of the groups were found. This corresponds to the findings of Aguilar-Rodríguez et al. (2001) that the majority of cloud forest species shows intermediate wood densities.

Tree geometry – Aboveground biomass (B) is calculated as

$$B(D) = \frac{\pi}{4} D^2 \cdot H(D) \cdot \frac{f\,\rho}{sw} \,,$$

with D being tree dbh, H being the height of the tree, f the form factor that corrects the deviation of the stem from the idealised conical shape, ρ the wood density, and sw the fraction of stem wood biomass from total tree biomass. Height (H) is calculated as

$$H(D) = \frac{D}{\frac{1}{h_0} + \frac{D}{h_1}} \,,$$

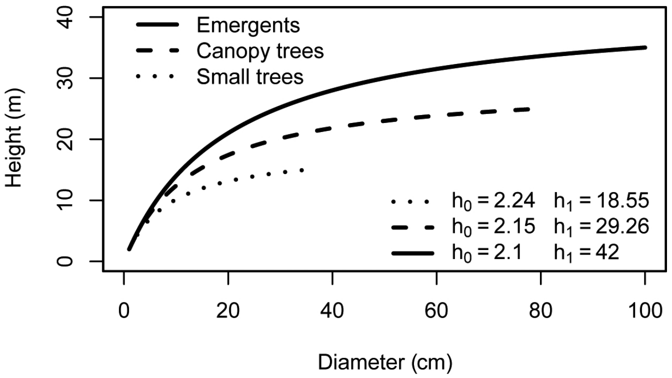

Figure 4.3 Relationship between tree diameter (at breast height) and tree height for the three height groups. h_0 and h_1 are parameter values of the diameter-height relationship. See text for details.

with h_0 and h_1 being parameters that were fitted to diameter and height measurements for single trees (Aguilar-Rodríguez et al. 2001, Fig. 4.3). The form factor f is estimated to be 0.5 in accordance with previous model parameterisations for tropical lowland forests (Köhler 2000). Stem wood biomass is assumed to account for 70% of total aboveground biomass, hence $sw = 0.7$. The crown of a tree is assumed to be a cylinder and the crown diameter to be proportional to the stem diameter. The ratio between stem diameter and crown diameter is estimated to be 1:20. In inventory data from central Veracruz the average diameter-crown diameter ratio of small trees was 1:23 (G. Williams-Linera, unpublished data), but the ratio seems to be lower for larger trees. The length of the crown is defined as one tenth of total tree height. If we use higher values, which might be more realistic, too many tree individuals are killed by the space competition mechanism (see Mortality). Leaf area index (L_{max}) for an individual tree is assumed to be 2.

Mortality – A basic mortality affects all trees randomly. Mortality rates are estimations based on the assumption that pioneer species have a higher mortality compared to late-successional species (e.g. Poorter and Arets 2003) and that mortality decreases with increasing maximum height. Estimated annual mortality rates are 5%, 1.5%, 1.5%, 1%, 0.8%, 1% for PFT 1 to 6, respectively. Small trees up to 10 cm dbh suffer additional mortality, which decreases linearly from 2.25% at 1 cm dbh to 0 at 10 cm dbh. Mortality due to crowding is included directly in the model. If in a given height layer the total crown area (of all trees with their crown in this height layer) exceeds the area of the grid cell, trees are removed randomly from the cell until the crown area is smaller than the area of the grid cell.

In Mexican cloud forests, trees die mainly through uprooting and less often through snapping or while standing (Bracho and Puig 1987, Williams-Linera 1991). In central Veracruz, the fraction of fallen dead trees was 84% (Williams-Linera 2002), in Tamaulipas 75% of the dead trees had fallen (Arriaga 1987). The majority of fallen trees belongs to upper canopy species that are taller than 15 m (Arriaga 1987, 2000) or to greater diameter classes (Williams-Linera 2002). Based on these data, in the model 80% of dying trees with > 35 cm dbh (PFTs 4, 5, 6) fall and damage the vegetation in the grid cell where their crown hits the ground. The damage is proportional to the crown area of the tree.

Recruitment – Every time step new individuals with a diameter of 1 cm appear if the available light at the forest floor is higher than the minimum light intensity required for establishment. Minimum light intensities for establishment were estimated to be 10% of full sun light for shade-intolerant PFTs, 3% for intermediate, and 1% for shade-tolerant PFTs. In shade-house experiments intermediate species grew well in 5% of full sun light (Álvarez-Aquino 2002). The number of new individuals is proportional to the available light at forest floor, with maximum ingrowth rates at full sunlight. We assume that seed numbers and hence ingrowth rates are higher for pioneer species compared to late-successional species. Maximum annual ingrowth rates are estimated to be 1000 ind/ha, 400 ind/ha, and 250 ind/ha for shade-intolerant, intermediate and shade-tolerant PFTs, respectively.

4.2.4 Simulations

To test the ability of the model to reproduce observed characteristics of old-growth forest in the study area, we use inventory data of five fragments (1000 m^2 each) of relatively undisturbed TMCF in central Veracruz (Williams-Linera 2002) as initial situation for a model run. We group the individuals according to their PFT and assign them to the corresponding diameter class (20 diameter classes of 5 cm). We run 10 simulations of the dynamics of 1 ha TMCF for 400 years. In the year 400, diameter distributions for the different PFTs are compared to the inventory data.

To simulate the regeneration of TMCF we start from a treeless area. We run 10 simulations of the dynamics of 1 ha TMCF for 400 years. We assume that seed input is not limited and that no further disturbances – other than gap creation by falling trees – occur during the course of succession.

4.3 Results

4.3.1 Comparison of model predictions with field observations

Simulation of old-growth forest – Figure 4.4 shows the simulated development of the old-growth forest using the inventory data as initial situation. At the beginning of the simulation period stem numbers (A) decline due to the lack of small individuals (< 5 cm dbh) in the inventory data, before they recover and fluctuate around the observed value. Total basal area (B) decreases by 10 m^2/ha, but the relative importance of PFTs remains. Simulated total stem numbers and basal area are found to be in the range of observations in the forest fragments of the study area (Table 4.2).

Diameter distributions – A more detailed inspection of model results can be carried out through comparison of diameter distributions of the different PFTs. Such a comparison ensures that the size structure of simulated and real forest is similar. Figure 4.5 shows stem number-diameter distributions of inventory data and simulated old-growth forest for all PFTs. For PFTs 5 and 6, which account for the largest trees and represent most of

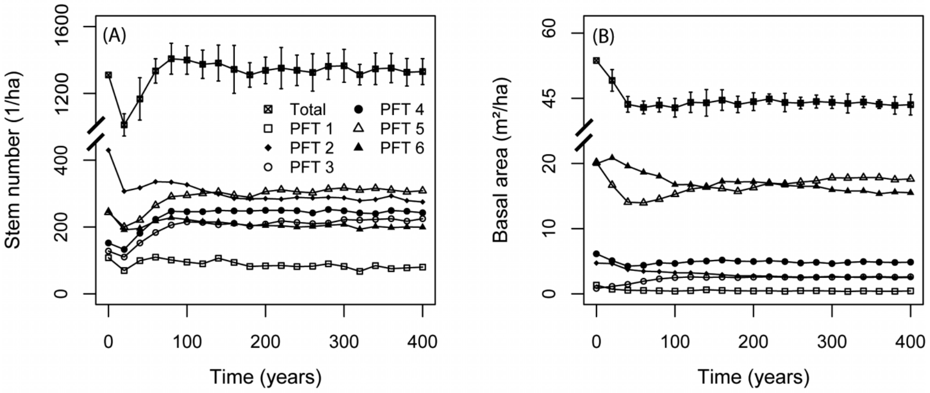

Figure 4.4 Simulation of the dynamics of old-growth forest. Inventory data (≥ 5 cm dbh) from five forest fragments (0.5 ha) are used as initial situation. Stem numbers (A) and basal area (B) are means of 10 simulations for 1 ha and 400 years (≥ 5 cm dbh). Standard deviation is shown for total stem numbers and basal area.

the forest's basal area, the diameter distributions are well reproduced. Similarly, mean and variability of stem numbers of pioneer species (PFT 1) are well captured. In the model, stem numbers for PFT 2 are underestimated, and overestimated for PFT 3 and PFT 4 in the smallest diameter class. However, these differences seem tolerable, especially when the high variability among the study sites is considered.

Other observations – Tree mortality in the model is caused by different processes, thus the resulting mortality rates are not known *a priori*. In field studies in the same forest fragments in central Veracruz, observed annual mortality rates ranged between 1 and 12% (Williams-Linera 2002; individuals ≥ 5 cm dbh, 2 years observation period, 0.1 ha). Mean annual mortality rate in the model is approximately 5.5%.

Table 4.2 Comparison of observed and simulated old-growth forest characteristics. Field observations mostly correspond to small areas (e.g. 0.1 ha), whereas simulation results are mean values for ten simulations (1 ha) and ten points in time.

Forest characteristics	Simulation	Observation	Reference
Total stem number[1]	1325 ind/ha	810 – 1700 ind/ha	Williams-Linera (2002)
Total basal area[1]	44 m²/ha	35 – 89 m²/ha	Williams-Linera (2002)
Mortality rate[1]	5.5%	1% – 12%	Williams-Linera (2002)
Available light on forest floor	10%	1% – 8.4%	Zuill and Lathrop (1975), Ramírez et al. (1998)
LAI	5	3.4 – 9.3	Hafkenscheid (2000), Fleischbein (2004)

[1] individuals ≥ 5 cm dbh

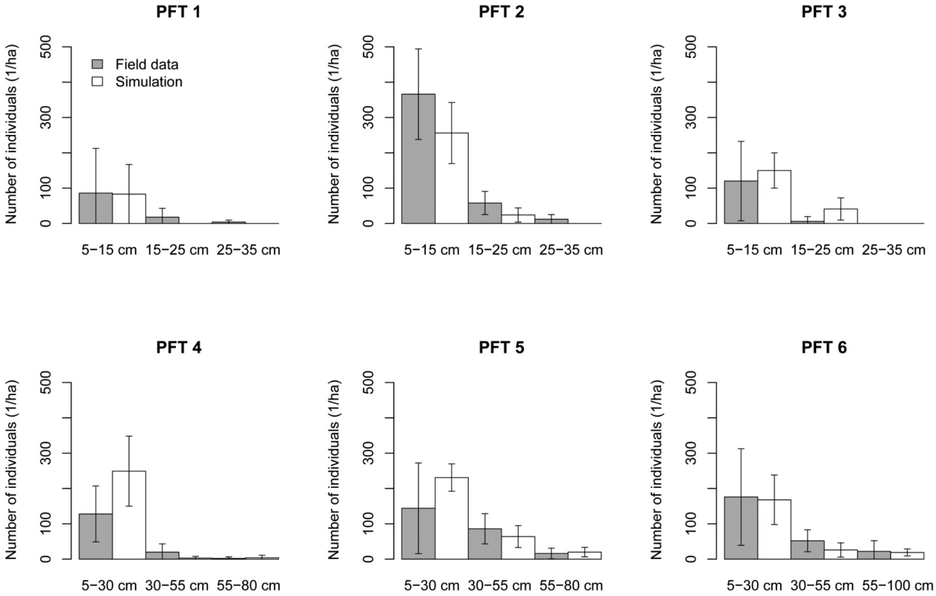

Figure 4.5 Measured and simulated stem number-diameter-distributions for the six plant functional types (PFT). Field data are means and standard deviations for five forest fragments (0.1 ha each). Simulated values are means and standard deviations for ten patches (0.1 ha each) of a simulated old-growth forest, i.e. after 400 years without large-scale disturbance.

In several studies, available light on the forest floor has been measured (Zuill and Lathrop 1975, Ramírez-Marcial et al. 1998). Zuill and Lathrop (1975) measured 1% in montane rain forest without deciduous species and 8.4% in Pine-Oak-Liquidambar forest. Ramírez-Marcial et al. (1998) measured 31 $\mu\text{mol(photons)}\cdot\text{m}^{-2}\text{s}^{-1}$ in TMCF, which corresponds to 5.2% of 600 $\mu\text{mol(photons)}\cdot\text{m}^{-2}\text{s}^{-1}$. The simulated mean percentage of the light available on the forest floor is approximately 10%, but this value also includes gaps.

In Ecuadorian lower montane forest, Fleischbein (2004) measured stand leaf area index (LAI) values ranging from 5.2 to 9.3. Hafkenscheid (2000) measured and predicted LAI values from 3.4 to 5 for different sites in an upper montane rain forest in Jamaica. Mean LAI of the simulated forest is approximately 5, which lies in the range of observed values (Table 4.2).

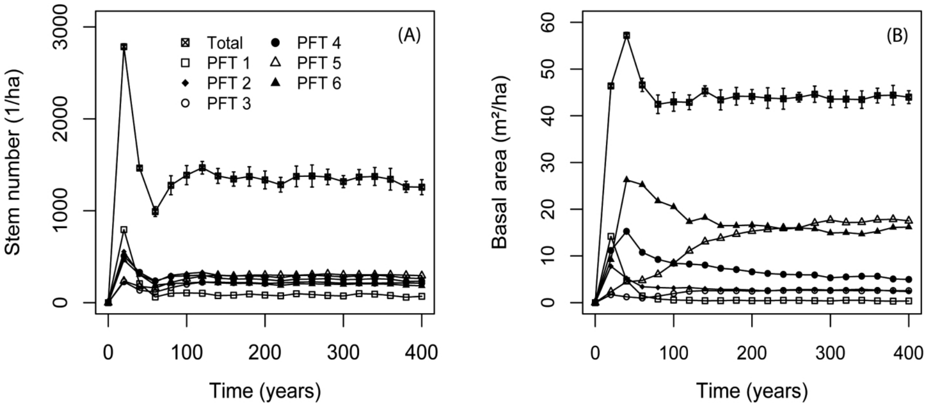

Figure 4.6 Simulation of forest regeneration after large-scale disturbance. Stem numbers (A) and basal area (B) are means of ten simulations for 1 ha and 400 years (individuals ≥ 5 cm dbh). Standard deviation is shown for total stem numbers and basal area.

Simulation of forest regeneration after disturbance 4.3.2.

Figure 4.6 shows the course of succession over 400 years, starting from a treeless area. Both, total stem numbers (≥ 5 cm dbh) and total basal area reach their steady state after approximately 80 – 90 years. Simulated stem numbers level off at approximately 1350 ind/ha. The total basal area fluctuates around 44 m^2/ha.

During the first twenty years all PFTs show a peak of stem numbers due to the high light and space availability. Pioneer species (PFT 1) account for most of the newly established individuals. Shade-tolerant PFTs (PFT 3 and 5) show the lowest stem numbers. Self-thinning already starts after ten years, and stem numbers rapidly decline to their steady state values. At steady state, pioneer species (PFT 1) are represented by only few individuals, because their establishment is possible only in gaps. All other PFTs maintain similar stem numbers.

The basal area has a different dynamics. During the first twenty years, pioneer species (PFT 1) account for most of the stand's basal area, due to their fast growth. Then they are rapidly replaced by PFTs with intermediate shade tolerance (PFTs 2, 4, 6), which reach their maximum basal area after approximately 50 years. PFT 5, the slow-growing shade-tolerant canopy species, is the last in arriving at its steady state basal area after approximately 300 years. Its increase in basal area is accompanied by a decrease of PFTs 4 and 6.

4.4 Discussion

The forest model FORMIND2.3 was parameterised for TMCF in central Veracruz, Mexico, to predict the course of succession of the cloud forest after large-scale disturbance. In this region, around 30% of the area is covered with secondary forests that re-grow after abandonment of agricultural fields or pastures. These regenerating forests can play an important role in providing ecosystem services, such as water capture from clouds, conservation of native biodiversity, soil protection, or provision of fuelwood for the local population. It is therefore important to know, how long the recovery of forest structure and composition will take. Before we applied the model, we tested it by comparing model outcomes with inventory data of old-growth forest fragments and other field observations (e.g. LAI, overall mortality rate, available light on forest floor). Simulation results indicate that structural variables (e.g. total stem number, basal area) recover during a few decades. However, the relative importance of PFTs continues to change until 300 years after disturbance.

4.4.1 Model parameters

We parameterised FORMIND on the basis of data on TMCF available in the literature, measurements carried out in the study area, experience gained during former model applications for tropical lowland rain forest, and parameter estimations of researchers who are well acquainted with central Veracruzan TMCF. However, there is information lacking and uncertainty remains about the true value of most parameters. Nevertheless, the model includes state-of-the-art knowledge on this forest type and its application can be justified. Not only can it help to detect gaps in knowledge, but also to investigate the importance of certain parameters for the questions addressed. This can be only fully investigated with a sensitivity analysis. During model parameterisation it already turned out that growth parameters (e.g. initial slope of light-response-curve) are important for the outcome of succession. It can thus be suggested to focus future field studies on growth characteristics (e.g. photosynthetic rate, respiration, and diameter increment) of important tree species. Especially, more information on diameter growth would help to adjust growth parameters.

4.4.2 Verification of model results

Comparison of simulation results with observed patterns confirmed that the simulated forests comply with typical characteristics of old-growth TMCF in central Veracruz. Inventory data of little disturbed old-growth forest constitute an important source of information on forest structure and composition. It is assumed that the inventory data of forest fragments used in this study represent the high variability of TMCF in this region. Some model parameters have been adjusted in a way that the model reproduces important characteristics of the inventory data. If it turns out that some of the fragments have been subject to major human disturbance in the past, the model parameterisation has to be revised. Currently, regeneration of TMCF in central Veracruz is being investigated using a chronosequence approach (M.A. Muñiz-Castro, pers. comm.). Results of this study will provide further possibilities to evaluate model predictions.

Forest regeneration 4.4.3

Recovery times of less than 100 years for aggregated variables have also been predicted for other tropical ecosystems. Hughes et al. (1999) estimate that aboveground biomass of a Mexican humid lowland forest would recover after 30 – 80 years after disturbance. Kammesheidt et al. (2001, 2002) simulate the regeneration of a logged-over forest stand in Venezuela and a young secondary forest in Paraguay. In both cases, variables that describe forest structure attain a steady state after 50 – 100 years. On the other hand, forest regeneration on nutrient-poor soils following slash-and-burn agriculture can take much longer. Saldarriaga et al. (1988) estimate recovery times of up to 200 years for the basal area and biomass of a mature forest in the Amazon basin. We simulated the regeneration of TMCF after a large-scale disturbance assuming unlimited seed dispersal and undisturbed regeneration. The assumption of unlimited seed dispersal may hold true for the TMCF region of central Veracruz, because diverse land use types with trees (e.g. forest fragments, shade-coffee plantations, pastures with trees) occur side by side. Furthermore, riparian corridors cut through the landscape and promote seed dispersal.

In the future, the model will be used to investigate the impact of selective logging on forest structure and composition. Selective logging is practised by the local rural population to meet their needs for fuelwood and it is unclear up to which intensity important forest characteristics, such as species composition, are preserved.

Conclusions 4.5

The process-based forest simulation model FORMIND contains the most important processes to successfully simulate TMCF dynamics after disturbance. With the presented model parameterisation we are able to reproduce relevant characteristics of TMCF in central Veracruz. We have shown this by comparison of several observed patterns with simulation results. Simulation of forest regeneration after disturbance suggests that aggregated variables, such as total stem number and total basal area, reach values of an old-growth forest after approximately 80 years, whereas the relative importance of PFTs continues to change until 300 years after disturbance. In the future, and after more extensive testing of the model behavior, the model can be applied to address questions such as long-term impacts of selective logging on forest structure and composition, and importance of previous land use for forest regeneration. The model results can support regional decision makers in forest conservation and restoration planning.

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"TALA HORMIGA"– SIMULATING LONG-TERM IMPACTS OF LOW-INTENSITY FUELWOOD EXTRACTION ON TROPICAL MONTANE CLOUD FOREST IN CENTRAL VERACRUZ, MEXICO*

Abstract

Fuelwood extracted from natural forests serves as main energy source in rural regions of many tropical countries. Despite its often low intensity, fuelwood extraction can have a strong impact on structure and species composition of natural forests. We study the long-term impacts of such repeated harvesting of single trees – in Mexico called "tala hormiga" – on tropical montane cloud forest in central Veracruz, Mexico. We apply the process-based forest growth model FORMIND to simulate forest dynamics under several logging scenarios and compare the structure and composition of simulated logged forest to those of simulated undisturbed old-growth forest. As knowledge on current use patterns is scarce, we simulate a wide range of possible scenarios differing in extracted wood volume (5 – 120 m^3/ha every 10 years), preferred tree species, and tree sizes.

When all canopy species are targeted and the minimum cutting diameter is 40 cm diameter (at breast height), up to 120 m^3/ha can be harvested every 10 years from the forest. Results show that impacts on forest structure and composition increase linearly with the amount of extracted wood volume. Even at low levels of harvesting, forest structure becomes simplified and more homogeneous in the long term, because large old trees that emerge over the main canopy disappear from the forest. With increasing levels of wood extraction, forests become "younger", i.e. the number of trees in larger diameter classes decreases whereas it increases for smaller diameter classes. Species composition shifts to tree species that are not used for fuelwood. These changes can take decades or even centuries.

If we are to minimise ecological impacts of fuelwood extraction from natural forests, our simulation results suggest that logging should target all canopy species to prevent shifts in species composition and that a few large old trees should be explicitly left in the forest as they provide important habitat for many plant and animal species. Forest models like FORMIND can support stake holders to design appropriate management strategies for natural forests, thus preventing the forests from undesired long-term degradation.

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5.1 Introduction

In many rural regions in the tropics, fuelwood is the most important energy source and fuelwood extraction from natural forests has a long tradition. In 2000, global fuelwood consumption was estimated to be 1616 million m^3 (Broadhead et al. 2001), and in Latin America alone 96 million people rely on biomass (mainly fuelwood and charcoal) for cooking and heating (International Energy Agency 2002). Often, the amount of wood harvested for fuelwood greatly exceeds harvested volumes for industrial purposes (e.g. Torres-Rojo 2004). In recent decades, population growth, accelerated forest conversion to agricultural fields or pastures and forest degradation led to increased pressure on the remaining forests to meet the needs for fuelwood and timber. In many cases, fuelwood extraction is carried out in an uncontrolled manner. Individual people or small associations of wood cutters carry out selective logging for home requirements for cooking and heating, local market supply of timber and fuelwood, or charcoal production. These logging activities account for a high proportion of wood extraction from tropical forests.

However, long-term consequences of such use schemes on structure and species composition of tropical forests are largely unknown. The majority of empirical studies on the effects of selective logging focus on high-intensity selective logging for valuable timber species. They study either responses of animal taxa to differences in habitat (e.g. Dunn 2004, Fredericksen and Fredericksen 2004, Dumbrell and Hill 2005, Holbech 2005) or the development of the tree community after the disturbance by logging (e.g. Okuda et al. 2003, Verburg and Eijk-Bos 2003). Fewer studies address impacts of single tree extraction of e.g. mahogany (*Swietenia macrophylla*) (Dickinson et al. 2000, Lambert et al. 2005). All these studies have in common that they investigate effects of a single logging operation. Modelling studies, on the other hand, often address the regeneration capacity of the tree community under different management scenarios and repeated timber harvesting. Most studies focus on commercial high-intensity selective logging for timber which is performed in relatively long intervals of several decades (e.g. Ditzer et al. 2000, Huth and Ditzer 2001, Kammesheidt et al. 2001, 2002, van Gardingen et al. 2003, Huth et al. 2005; but see Sist et al. 2003, Gourlet-Fleury et al. 2005 for intermediate and low logging intensities).

There are only few studies on continued forest disturbance by logging for fuelwood by local people. Some of these studies indicate that fuelwood and timber extraction might not be sustainable, and forests are showing signs of degradation (e.g. Sundriyal and Sharma 1996, Holder 2004, McCrary et al. 2005). A sustainability assessment of logging practices is complicated as high levels of illegal logging make access to information on amount of extracted wood, applied logging practices, and preferred species difficult. Furthermore, the comparably low use intensity results in slow ecosystem changes which can only be observed over several decades or even centuries. Therefore, short-term research projects will often have difficulties to detect effects of low-intensity fuelwood extraction.

We apply the process-based forest growth model FORMIND (e.g. Köhler and Huth 1998, Köhler et al. 2001) to simulate long-term dynamics of tropical montane cloud forest (TMCF) in central Veracruz, Mexico, which is disturbed by repeated low-intensity selective logging for fuelwood. In Mexico, the estimated annual fuelwood consumption is 36 million m^3 which is almost twice as much wood as is harvested for industrial purposes (Torres-Rojo 2004). Approximately 25 million people in Mexico depend on fuelwood (Masera et al. 2004). Local patterns of fuelwood use are very heterogeneous and an analysis of fuelwood consumption and availability in Mexico has classified 46% of all municipalities as medium to high priority areas, indicating high fuelwood use in these areas (Masera et al. 2004). In the recent past, population growth and deforestation have caused increased pressure on forests, and it is seriously questioned if current levels of fuelwood extraction are sustainable. Until now, there are almost no rationally managed second-growth forests or plantations of native tree species to ensure the supply of sufficient fuelwood to the population. 45

In central Veracruz, the study area of this project, the area covered by TMCF has decreased rapidly over the last 50 years (Williams-Linera et al. 2002). Deforestation has been accompanied by the fragmentation of the remaining forest and almost all remaining forest fragments are permanently disturbed by selective logging for fuelwood. This low-intensity wood extraction is locally called “tala hormiga”, literally translated as “ant extraction”. Large living trees are felled with chainsaws, directly cut into pieces within the forest, and extracted with the help of pack animals. Preferred tree species for fuelwood include oaks (*Quercus* spp.), hornbeam (*Carpinus caroliniana*), sweetgum (*Liquidambar styraciflua*), *Clethra mexicana*, and *Alnus acuminata* (Haeckel 2006).

The forest model FORMIND is individual-oriented and calculates the carbon balance for each individual tree on the basis of the light climate in the forest. Thus, it allows for detailed incorporation of different selective logging strategies, targeting special species groups and tree sizes or applying different harvesting intensities. For these different logging strategies, we assess changes in structure and species composition of the tree community over several hundred years. To our knowledge, this study is the first attempt to determine long-term effects of repeated selective wood harvesting on a moist tropical forest by applying a process-based simulation model. Although model results are specific to Mexican TMCF, we believe that they indicate tendencies that will also apply to other tropical moist forests disturbed by comparable logging practices. With our assessment of ecological long-term implications of different low-intensity selective logging strategies we aim to contribute to an improved understanding of long-term ecosystem dynamics under anthropogenic disturbance as well as to a sustainable use of the native forest resources.

5.2 Methods

5.2.1 Study sites

Five forest fragments in the TMCF region of central Veracruz, Mexico (19°30′ N, 96°54′ W) were selected for this study. The sites are located at an altitude between 1250 and 1875 m. The climate is mild and humid throughout the year with three seasons. A relatively dry-cool season extends from November to March, a dry-warm season from April to May, and a wet-warm season from June to October. Annual precipitation varies between 1350 and 2200 mm; mean annual temperature is between 12 and 18°C (Williams-Linera 2002). The soil has been classified as Andosol (Rossignol 1987). The number of observed trees species > 5 cm diameter at breast height (dbh) varies between 16 and 28 at the five study sites. Dominant tree species include *Carpinus caroliniana*, *Clethra mexicana*, *Fagus grandifolia*, *Liquidambar styraciflua*, *Quercus germana*, *Q. leiophylla*, *Q. xalapensis*, and *Turpinia insignis* (Williams-Linera 2002).

To enable an individual-based simulation of forest dynamics, the 58 native tree species that occur at the study sites were grouped into plant functional types (PFT). Criteria for classification into PFTs were light demand and maximum attainable height. Three levels of shade tolerance were distinguished (shade-intolerant (i), intermediate (m), and shade-tolerant (t)). Three height groups were considered: small trees (≤ 15 m tall, ≤ 35 cm dbh), canopy trees (≤ 25 m tall, ≤ 80 cm dbh), and emergent trees (≤ 35 m tall, ≤ 100 cm dbh). This classification resulted in six PFTs because some of the combinations are rare (Table 5.1).

Table 5.1 Definition of plant functional types (PFTs) according to shade tolerance (T) and maximum attainable height (H_{max}). Three levels of shade tolerance are distinguished: i = shade-intolerant, m = intermediate, t = shade-tolerant. The successional status refers to the stage of succession in which a PFT attains maximum basal area values.

Plant functional type	PFT	T	H_{max}	Examples
Early successional small trees	1	i	15 m	*Heliocarpus*, *Myrsine*
Mid successional small trees	2	m	15 m	*Miconia*, *Oreopanax*
Late successional small trees	3	t	15 m	*Cinnamomum*, *Ilex*
Mid successional canopy trees	4	m	25 m	some *Quercus* spp.
Late successional canopy trees	5	t	25 m	*Magnolia*, *Beilschmiedia*
Emergents	6	m	35 m	*Liquidambar*, *Clethra*

The process-based forest growth model FORMIND 5.2.2

The model description follows the ODD protocol which has been proposed as a standard protocol for describing individual- and agent-based models (Grimm and Railsback 2005, Grimm et al. in press). A more detailed description of the mathematical formulation of ecological processes, and a table with model parameters is provided in Appendix A. Details on model parameterisation for TMCF in central Veracruz, Mexico can be found in chapter 4.

Purpose – The individual-oriented forest growth model FORMIND was developed to study the long-term response of uneven-aged mixed species rain forests to natural or anthropogenic disturbances such as wind throw, logging, or fragmentation (e.g. Köhler and Huth 1998, Köhler 2000, Köhler et el. 2001, Kammesheidt et al. 2002, Köhler et al. 2003, Köhler and Huth 2004, Huth et al. 2005).

State variables and scales – FORMIND is a three-dimensional, grid-based, individual-oriented model. It formulates the ecological processes on three hierarchical levels: tree cohorts, grid cells (below called patches) and hectares. To enable an individual-based simulation of the dynamics of species-rich forests, tree species that occur at the study sites are grouped into plant functional types (PFT) with similar shade tolerance and maximum attainable height. All trees that belong to the same PFT, and that establish in the same year in the same patch are grouped into a cohort. All trees in one cohort are equal in size. Trees with a diameter > 40 cm are usually simulated individually, because all other trees from their cohort have died. Each tree cohort is characterised by the state variables PFT, number of individuals, above-ground biomass of one individual, and position (i.e. the patch where the cohort is located). From the biomass of the tree all other morphological variables of the tree such as diameter at breast height (dbh), height, crown diameter, crown depth, and stem volume are derived.

A patch is characterised by the tree cohorts present in the patch, and its coordinates within the hectare where the patch is located. The size of a patch corresponds to the crown size of mature trees (here 20 m × 20 m). Leaf area of the trees is added up in small horizontal layers, and the available light is calculated for each layer. Neighbourhood relations link each patch to its four direct neighbours (across hectare boundaries) to allow dying trees to fall into another patch.

Finally, hectares are characterised by the patches they comprise, and they contain higher-level information on overall logging potential (i.e. the number and stem volume of harvestable trees) of all patches that belong to the hectare. Hectares are arranged spatially as a square, such that the simulation area necessarily is a square number of hectares. Minimum extent of the simulation area is one hectare, and several hundreds of hectares can be simulated. The simulation area is simulated as a torus (i.e. with periodic boundary conditions). The model simulates a forest in annual time steps and simulation runs usually comprise several hundred years.

Process overview and scheduling – It is assumed that light availability is the main driving force for individual tree growth and forest succession. Within each patch all trees compete for light and space following the gap model approach (Shugart 1998). The light climate in each patch is calculated via an extinction law depending on the vertical distribution of the leaf area of the trees in the patch (Monsi and Saeki 1953). Depending on the resulting light climate, the light availability is determined for each tree. Annual growth of each tree is calculated on the basis of the main physiological processes, i.e. photosynthesis and respiration, and litter fall. Growth process equations are partly taken from the model FORMIX3-Q (Ditzer et al. 2000). Allometric functions relate above-ground biomass, stem diameter, tree height, crown diameter, and stem volume. Tree mortality can occur either through self-thinning in dense patches, stochastic mortality, or gap creation by large falling trees. Recruitment occurs when the light intensity at forest floor exceeds a PFT-specific threshold. Recruitment rates describe the number of small trees growing over the dbh threshold of 1 cm per year.

Within each year – or time step – five modules are processed in the following order: recruitment, mortality, re-calculation of the light climate in the forest interior, growth, and logging. Recruitment, calculation of light climate, and logging are executed for each patch, whereas growth and mortality are determined for each tree cohort.

Initialisation – For the logging scenarios we use inventory data of old-growth TMCF from the study sites as initial forest state. These inventory data are expanded to correspond to the simulation area of 81 ha and individual trees are randomly distributed among the different patches.

Input – Site conditions are assumed to be homogeneous and there is no inter-annual variability of environmental conditions.

5.2.3 Model evaluation

The ability of the model to reproduce observed forest characteristics of old-growth TMCF on different hierarchical levels has been extensively tested in a previous study of forest succession after large-scale disturbance (Rüger et al. in press). It has been verified that simulated maximum diameter increment, stem numbers, basal area and diameter distributions for the six PFTs, leaf area index (LAI) and overall mortality rate for the entire tree community, as well as available light at forest floor correspond to field measurements from the study site or lie in the range of values reported for other TMCF sites.

Here, we check additionally if above-ground biomass (dry mass) of single trees derived from geometric equations of FORMIND match field measurements. For the study area only few empirical data on tree biomass or wood volume were available, and those were exclusively for small trees < 25 cm dbh that belong to PFT 1 (Acosta-Mireles et al. 2002). Thus, empirical biomass equations for North American congeners were used to complement the comparison (Ter-Mikaelian and Korzhukin 1997). For PFT 5, we used empirical equations for *Fagus grandifolia*, because *F. grandifolia* var. *mexicana* which occurs in the study sites was classified as PFT 5. For PFTs 4 and 6, we used biomass equations for North American *Quercus* spp., because the oak species from the study sites were mainly classified as PFTs 4 and 6. Thus, an evaluation of tree biomass values was only carried out for PFTs 1, 4, 5 and 6. However, PFT 2 and 3 comprise small trees with a maximum dbh of 35 cm, and do not contribute substantially to overall biomass.

Selective logging of old-growth forest 5.2.4

We simulated selective logging scenarios of old-growth TMCF by varying the extracted stem volume between 5 and 100 m³/ha with a logging cycle of 10 years to study current logging practices with low logging intensities. There are few data available on actual wood extraction. For this reason, we varied the logging intensity in a broad range to investigate potential effects. Total standing wood volume of an undisturbed old-growth forest is ca. 500 m³/ha, thus 1 – 20 % of total wood volume is extracted every 10 years by the logging scenarios. 100 m³/ha correspond to 23 – 47 trees/ha depending on the average dbh of logged trees, and this rather high logging intensity was simulated to study the potential of the forest for wood extraction. We used inventory data as initial condition and then simulated forest dynamics over a 100 years time period to allow the model to establish a steady state old-growth forest. Selective logging scenarios were then applied over a simulation time of 400 years (i.e. time steps 100 – 500 in the model).

Four selective logging scenarios were simulated (Table 5.2). In the first two scenarios (*S1*, *S2*), only trees of PFT 4 and 6 were logged, because preferred tree species for fuelwood (e.g. *Quercus* spp., *L. styraciflua*, *C. caroliniana*, *C. mexicana*) were mainly classified as PFTs 4 and 6. Scenarios *S3* and *S4* applied logging to PFT 4, 5, and 6. In scenarios *S1* and *S3*, logging concentrated on medium-sized trees with a dbh of 40 – 60 cm which are preferentially cut in the study area for fuelwood and charcoal production for local market supply (G. Williams-Linera, pers. observation). Scenarios *S2* and *S4* allowed cutting of all trees > 40 cm dbh. If at a given time step the stem volume of all harvestable trees in the simulation area did not reach the volume value aimed by the logging scenario, the respective logging operation was omitted. This was done to keep logging scenarios comparable and to clearly reveal the limits of a sustained fuelwood extraction. Felled trees were directed to already existing gaps if possible. Apart from trees that were killed by the falling tree, no additional logging damages were considered because wood extraction in the study area is carried out without heavy machinery with the help of pack animals.

Logged plant functional types (PFT) and diameter ranges used in simulations of selective logging scenarios. PFT 4 = mid successional canopy trees, PFT 5 = late successional canopy trees, PFT 6 = mid successional emergent trees. **Table 5.2**

Scenario	Logged PFT	Diameter class (cm)
S1	4, 6	40 – 60
S2	4, 6	> 40
S3	4, 5, 6	40 – 60
S4	4, 5, 6	> 40

5.2.5 Assessment of logging scenarios

To evaluate the economic and ecological implications of a logging scenario we calculated five variables, namely total yield (*Y*), percentage of omitted logging operations (*PO*), an index of structural change (*ISC*), an index of compositional change (*ICC*), and leaf area index (*LAI*). *Y* and *PO* are economic indicators of amount and continuity of wood harvest, *ISC* and *ICC* are ecological indicators of forest structure and species composition, and *LAI* is an environmental indicator of the potential of the forest to capture water from clouds and protect the soil from erosion.

Y and *PO* were calculated for each scenario over the simulation period 100 – 500 years. *ISC* was calculated as

$$ISC = \frac{1}{5}\sum_{i=1}^{5}\frac{|\bar{x}_{s_i} - \bar{x}_{c_i}|}{\bar{x}_{c_i}} ,$$

i.e. the differences in mean tree numbers (simulation time 400 – 500) of five different diameter classes ($i = 1$: 5 – 20 cm, $i = 2$: 20 – 40 cm, $i = 3$: 40 – 60 cm, $i = 4$: 60 – 80 cm, $i = 5$: 80 – 100 cm dbh) of a simulated logged forest ($\bar{x}_{s_i}$, $i = 1 – 5$) in comparison to a simulated old-growth forest ($\bar{x}_{c_i}$, $i = 1 – 5$) where no logging had been applied. *ICC* indicates the change in relative importance of PFTs of the logged forest in relation to an undisturbed old-growth forest based on importance values (*IV*). Importance values of the different PFTs (IV_i, $i = 1 – 6$, for a description of PFTs see Table 5.1) were calculated as

$$IV_i = \frac{ba_i}{ba_{total}} + \frac{n_i}{n_{total}} ,$$

i.e. the sum of the relative basal area (*ba*, m^2/ha) and relative density (*n*, trees/ha) of trees ≥ 5 cm dbh of the focal PFT in relation to all PFTs (*total*). *ICC* was then calculated as

$$ICC = \frac{1}{6}\sum_{i=1}^{6}\frac{|\overline{IV}_{s_i} - \overline{IV}_{c_i}|}{\overline{IV}_{c_i}} ,$$

i.e. summing the differences between the mean *IV*s of PFT *i* from the logging scenario ($\overline{IV}_{s_i}$) and the mean *IV*s from the control scenario $\overline{IV}_{c_i}$, and dividing it by the mean *IV*s of PFT *i* from the control scenario $\overline{IV}_{c_i}$ for simulation time 400 – 500. *LAI* values were directly determined from model output and averaged over the simulation time 400 – 500.

For comparison of logging scenarios with other land covers/land uses, we also calculated *Y*, *ISC*, *ICC*, and *LAI* for bare ground (without trees), simulated undisturbed old-growth forest (simulation without logging), simulated intensively managed young secondary forest (PFTs 4 and 6), and a simulated even-aged plantation of only PFT 6. The secondary forest is dominated by PFTs 4 and 6, and regeneration of other species is prevented. Management consists in logging approximately 60 m^3/ha every 5 years. The plantation is clear cut every 25 years. *ISC*, *ICC*, and *LAI* are averaged for each scenario for a period of 100 years.

To contrast economic benefit and ecological impact of a logging scenario, we calculated an ecological index (*EI*), which measures the similarity of a logged forest to undisturbed old-growth forest, and a yield index (*YI*). *EI* includes the ecological variables *ISC*, *ICC*, and *LAI*, which were divided by the maximum value obtained from all logging scenarios (ISC_{max}, ICC_{max}, LAI_{max}) and summed up:

$$EI = \frac{1}{3}\left(\left(1 - \frac{ISC}{ISC_{max}}\right) + \left(1 - \frac{ICC}{ICC_{max}}\right) + \frac{LAI}{LAI_{max}}\right).$$

YI represents the yield of a scenario relative to the maximum yield obtained from all logging scenarios (Y_{max}): 51

$$YI = \frac{Y}{Y_{max}}.$$

Results 5.3

Tree biomass 5.3.1

For PFT 1, biomass values calculated by FORMIND corresponded well with empirical equations (Fig. 5.1). For PFT 4, biomass values calculated by FORMIND fell well in the range of reported empirical equations up to a dbh of 50 cm. No field data were available for trees beyond this size. For PFT 5, field measurements were available up to 66 cm dbh. Biomass values calculated by FORMIND were at the upper limit of empirical biomass equations. The same occurred for PFT 6. There were no biomass data available for trees with large diameters. Overall, FORMIND tended to slightly overestimate biomass values. This trend may become more pronounced for large trees > 50 cm dbh.

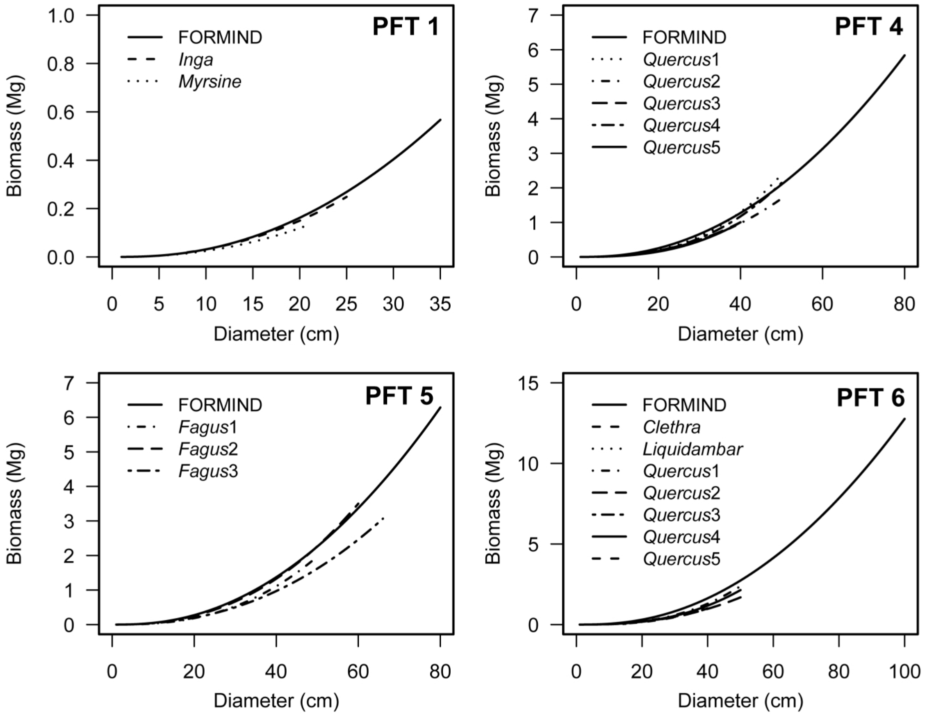

Figure 5.1 Biomass (Mg dry mass) of single trees of PFTs 1, 4, 5, and 6 (see Table 5.1) calculated with FORMIND 2.3 and empirical biomass functions taken from Ter-Mikaelian and Korzukhin (1997) and Acosta-Mireles et al. (2002). For PFTs 2 and 3 no field data were available.

5.3.2 Example simulations

For illustration, we show the temporal development of undisturbed old-growth forest and of one logging scenario (Fig. 5.2). In the control scenario, the case without wood extraction, stem numbers decline during the first 20 years due to the lack of small trees (< 5 cm dbh) in the inventory data which were used as initial situation (Fig. 5.2A). After 80 years a steady state is reached which corresponds well to field data for total stem numbers and stem numbers of PFT 1. For PFTs 2 and 6, simulated stem numbers are lower than observed stem numbers at the study sites, whereas they are higher than observed for PFTs 3, 4, and 5. However, stem numbers are dominated by small trees which do not determine overall forest structure. In terms of basal area, simulated basal area values are slightly lower than at the study site for PFTs 5 and 6, and hence also for total basal area (Fig. 5.2B). Figures 5.2C, D show simulation results when 45 m^3/ha are harvested every 10 years. Logging started after 100 years and targeted medium-sized trees (40 – 60 cm dbh) of PFTs 4, 5, and 6. Stem numbers increase due to the higher light availability, but basal area decreases by 5 m^2/ha compared to the control scenario. The decrease affects mainly PFTs 5 and 6, whereas basal area of PFT 4 increases.

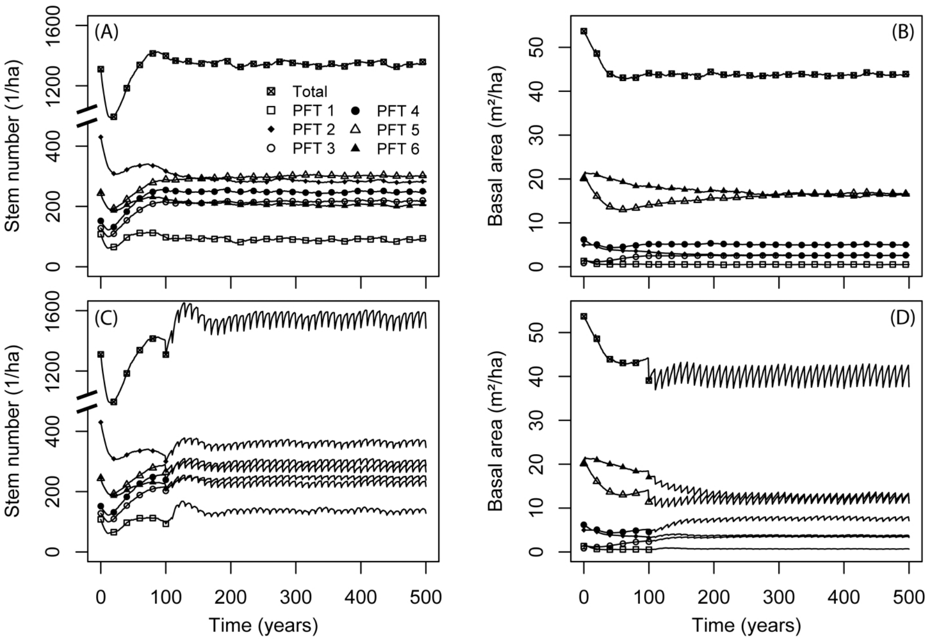

Figure 5.2

Stem numbers and basal area of undisturbed old-growth forest (A, B) and when 45 m^3/ha are extracted every 10 years under logging scenario S3 (C, D; see Table 5.2 for a description of logging scenarios). Inventory data ($\geq$ 5 cm dbh) from five forest fragments (0.5 ha) were used as initial situation. Stem numbers and basal area are means for a simulation area of 81 ha (individuals $\geq$ 5 cm dbh).

5.3.3

Total yield

Total yield (Y) over the 400 year period of logging is shown in Figure 5.3. When only trees of PFT 4 and 6 were logged (scenarios *S1* and *S2*), only 20 and 30 m^3/ha could be extracted from the forest every 10 years, respectively. Beyond this threshold, the number of omitted logging events increased sharply for scenario *S1*, and gradually for *S2*. When the diameter range of logged trees was restricted to 40 – 60 cm dbh (*S1*), volumes higher than 50 m^3/ha could never be achieved, and thus no logging took place in these scenarios. If volumes > 30 m^3/ha were to be logged under scenario *S2*, the time lags between two logging events had to be prolonged, and total yield saturated at ca. 1380 m^3/ha for the 400 year period. When all canopy species (PFT 4, 5, and 6) were harvested (*S3*, *S4*), total potential yield increased. When only trees with 40 – 60 cm dbh were logged (*S3*), up to 45 m^3/ha could be repeatedly logged every 10 years. In the case without diameter limit (*S4*), up to 120 m^3/ha could be harvested from the forest every 10 years (> 100 m^3/ha not shown). Note: For clarity reasons, the following results present only analyses of those cases where logging intensities could be achieved without omitting any logging events, i.e. 5 – 20 m^3/ha for *S1*, 5 – 30 m^3/ha for *S2*, 5 – 45 m^3/ha for *S3*, 5 – 100 m^3/ha for *S4*. Since the logging target was not always met exactly (because you can only harvest whole trees), we display results in relation to mean yield per cut (i.e. every 10 years).

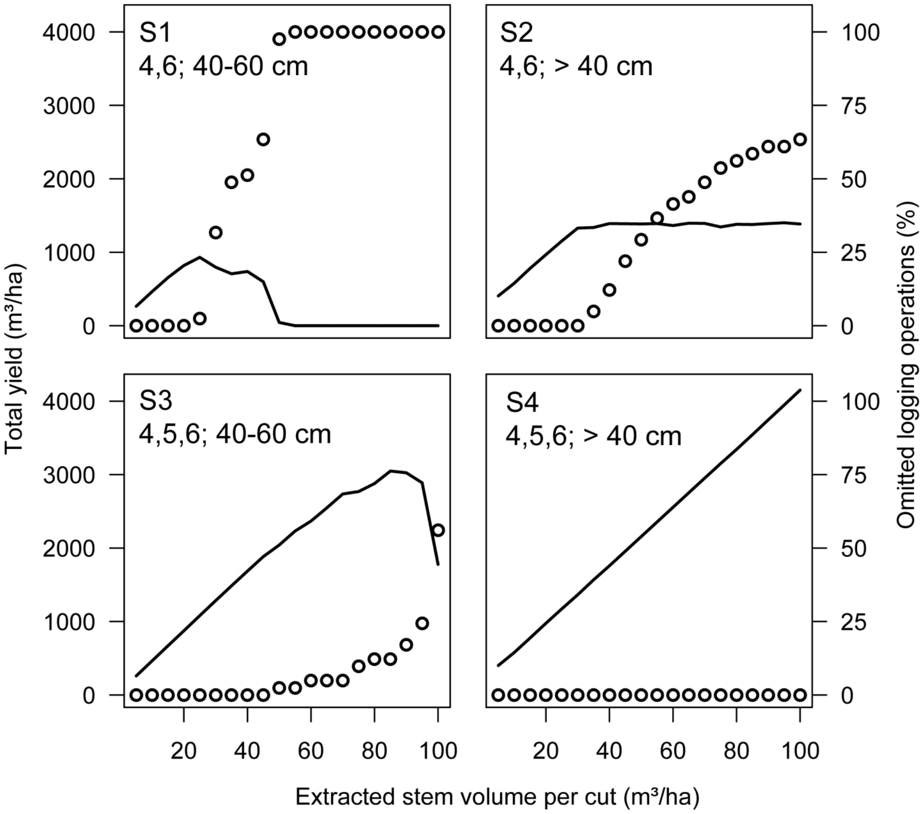

Figure 5.3 Total yield (Y, lines) and percentage of omitted logging operations (*PO*, circles) for four selective logging scenarios (*S1* – *S4*, see Table 5.2). Logging intensity varies from 5–100 m³/ha that are harvested every 10 years for a simulation period of 400 years.

5.3.4 Forest structure and composition

Figure 5.4 shows the changes of stem numbers in five diameter classes for the four logging scenarios. Stem numbers in the two smallest diameter classes (5 – 20 cm and 20 – 40 cm dbh) increased with increasing wood extraction for all scenarios (Fig. 5.4A, B). The intermediate diameter class (40 – 60 cm dbh) was the only diameter class directly affected by logging under scenarios *S1* and *S3*. Here, a decline of stem numbers was observed for scenarios *S1* and *S3* (Fig. 5.4C). For *S2*, stem numbers remained constant for low levels of wood extraction and slightly decreased for higher levels. For *S4* stem numbers increased up to a mean yield of ca. 75 m³/ha and then sharply declined. Stem numbers in the 60 – 80 cm dbh class increased for scenarios *S1* and *S2*, because they benefited from the decrease of emergent trees in the largest dbh class (Fig. 5.4D). For scenarios *S3* and *S4* they declined, in the case of *S4* to very low numbers for high levels of wood extraction. When *S4* was simulated with wood extraction levels >95 m³/ha, no trees >60 cm dbh remained in the forest. The strongest impact of logging scenarios was observed for the largest size class which only contained emergent trees of PFT 6 (80–100 cm dbh; Fig. 5.4E). Even at low levels of wood extraction stem numbers decreased sharply for all scenarios. For scenario *S3*, the decline occurred slightly more slowly with increasing wood extraction and under this scenario more large trees were maintained in the forest compared to the other scenarios. Examination of stem numbers of large old trees (60–100 cm dbh) over time revealed that the slow decline could take up to 100 years, here shown for the case where 45 m³ of wood volume were extracted under the *S3* scenario (Fig. 5.5).

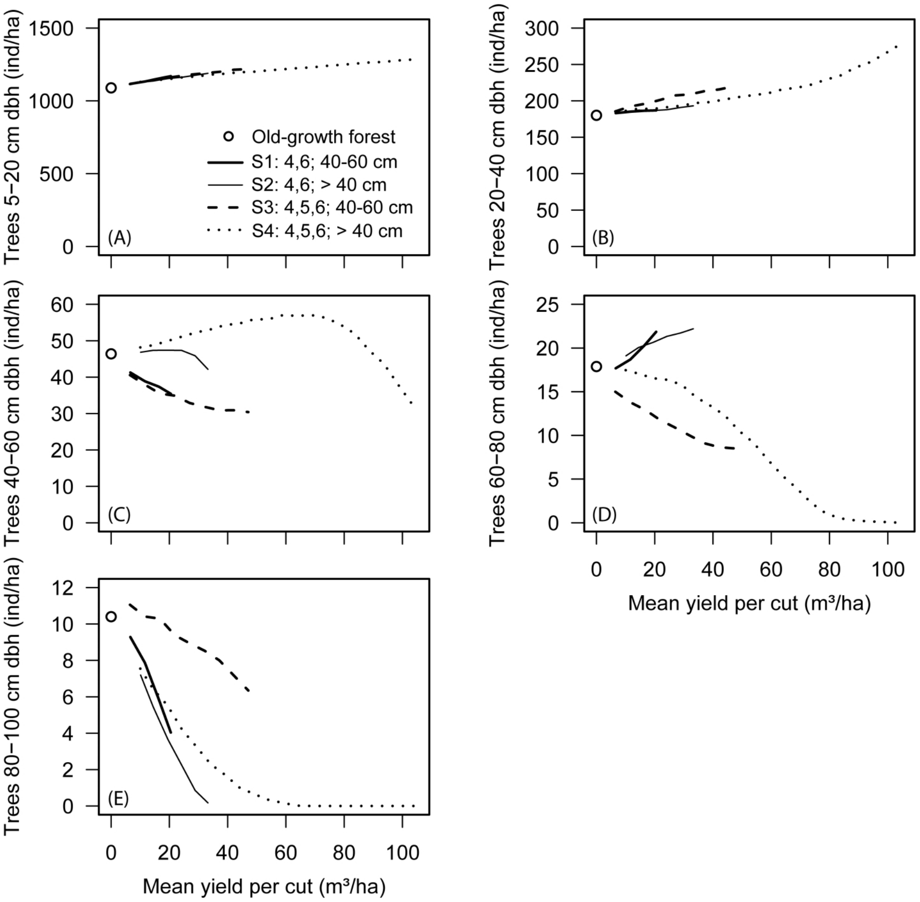

Figure 5.4

Mean number of trees in five diameter classes for simulation time 400–500 for four selective logging scenarios (*S1*–*S4*, see Table 5.2); trees with (A) 5–20 cm dbh, (B) 20–40 cm dbh, (C) 40–60 cm dbh, (D) 60–80 cm dbh, (E) 80–100 cm dbh. Mean values for undisturbed old-growth forest are displayed for comparison (o).

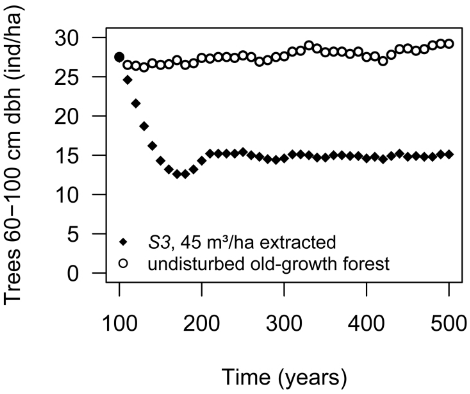

Figure 5.5 Mean number of large trees (60 – 100 cm dbh) for simulation time 100 – 500 for scenario *S3* where 45 m³/ha wood volume was extracted. For a description of logging scenarios see Table 5.2.

LAI of the entire forest stand varied only slightly among scenarios (range 4.3 – 4.7) and was only slightly lower than in simulated undisturbed old-growth forest (5.7).

The detailed impact of the logging scenarios on the species composition is shown in Figure 5.6. In scenarios *S1* and *S2*, PFT 5 increased with increasing wood extraction in importance mainly at the expense of PFT 6, which is subject to logging. Scenarios *S3* and *S4* reduced the importance of PFT 5 and 6, whereas the smaller tree species (PFT 2 and 3) and PFT 4 increased. A slight increase of pioneer species (PFT 1) was observed for all scenarios except for *S1*.

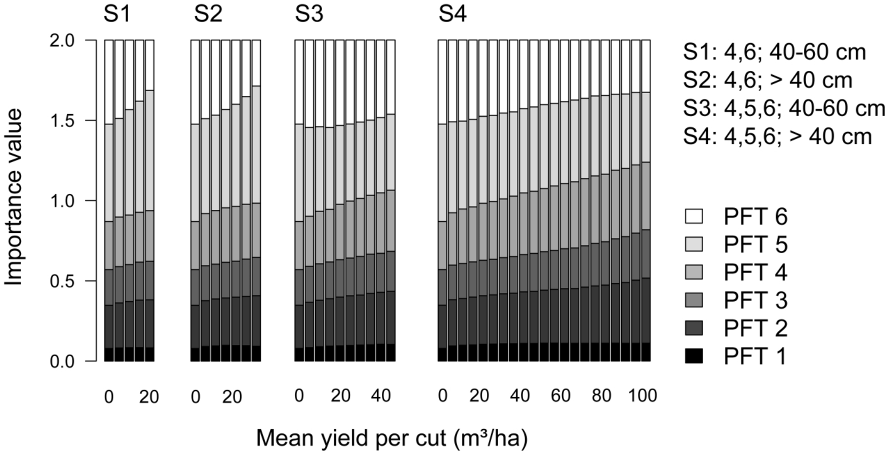

Figure 5.6 Importance values (*IV*, relative density + relative basal area of PFT, see section 5.2.5 *Assessment of logging scenarios* for details) as a measure of dominance of six PFTs for four selective logging scenarios (*S1* – *S4*). See Table 5.1 for a description of PFTs and Table 5.2 for a description of logging scenarios. Importance values of the undisturbed old-growth forest are displayed for comparison (0 m³/ha).

The index of structural change (*ISC*) combines the changes in stem numbers in the five diameter classes to assess the overall impact of the different logging scenarios on forest structure. For all scenarios, *ISC* almost linearly increased with increasing wood extraction (Fig. 5.7A). *S1* and *S2* had a proportionally higher impact on forest structure than *S3* and *S4*.

The change in species composition of the logged forest, compared to undisturbed old-growth forest, is summarised in the index of compositional change (*ICC*) (Fig. 5.7C). For all logging scenarios, *ICC* also increased nearly linearly with extracted wood volume. However, the increase of *ICC* was steeper for scenarios *S1* and *S2* than for *S3* or *S4*, because in *S1* and *S2* only two of the main canopy PFTs were targeted by logging, and hence species composition was altered more than proportionally.

In terms of forest structure, the simulated logging scenarios approach the structure of an intensively managed young secondary forest at high logging intensities (Fig. 5.7B). In comparison, even-aged plantations are structurally very different. Looking at species composition, selectively logged old-growth forests are still much more similar to undisturbed old-growth forest than intensively managed secondary forests or monospecific plantations (Fig. 5.7D).

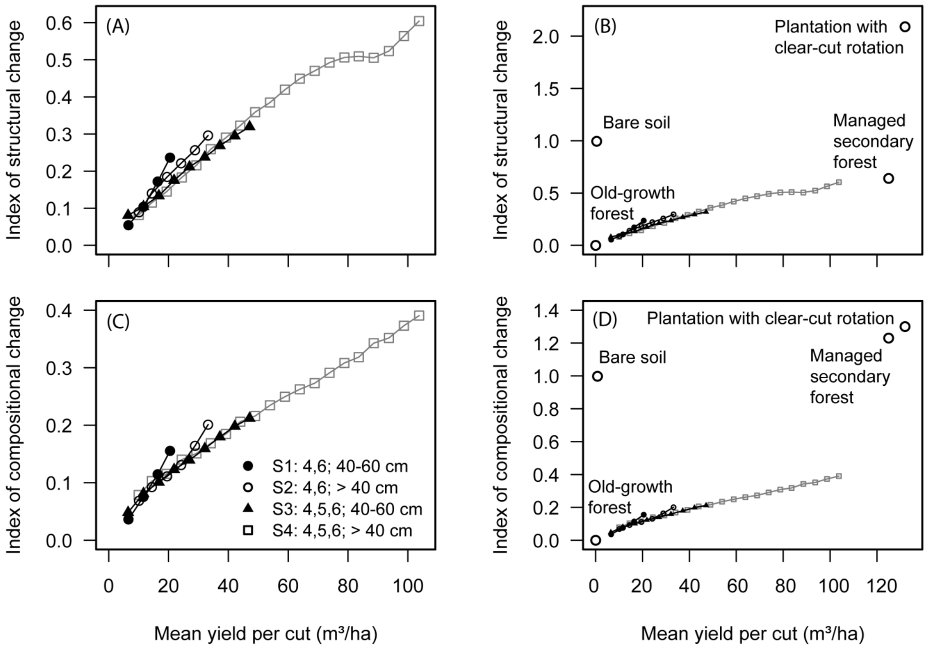

Figure 5.7

Index of structural change (*ISC*, A, B) and index of compositional change (*ICC*, C, D) for four selective logging scenarios (*S1 – S4*, see Table 5.2). *ISC* and *ICC* values of undisturbed old-growth forest, bare ground, intensely managed secondary forest dominated by PFT 4 and 6, and an even-aged monospecific plantation of PFT 6 with clear-cut rotation in 25-year cycles are shown for comparison (B, D).

With increasing yield, similarity to undisturbed old-growth forest (*EI*) decreased almost linearly for all logging scenarios (Fig. 5.8A). Hence, every surplus in yield is accompanied by an increase of ecological impact. For scenarios *S1* and *S2*, the decrease was sharper than for *S3* and *S4*, due to their stronger impact on species composition. Compared to other forms of forest management (managed young secondary forests and plantations), however, selective logging of old-growth forest is relatively benign (Fig. 5.8B). This is mainly due to the conservation of all PFTs in the forest.

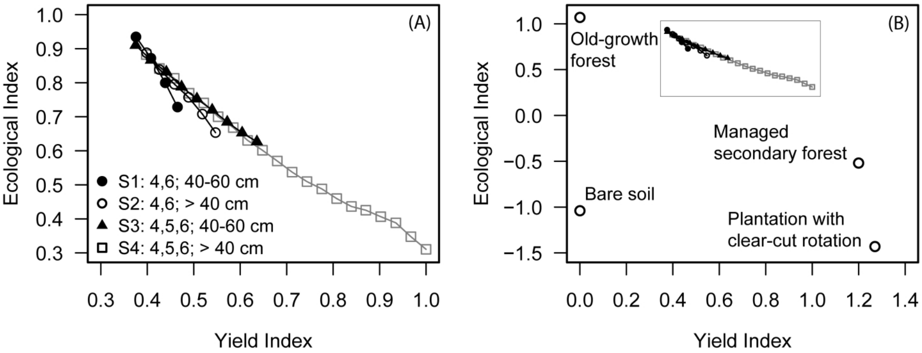

Figure 5.8 Ecological Index (*EI*) versus Yield Index (*YI*) for (A) four selective logging scenarios (*S1* – *S4*, see Table 5.2) and (B) in the context of undisturbed old-growth forest, bare ground, intensely managed secondary forest dominated by PFT 4 and 6, and an even-aged monospecific plantation of PFT 6 with clear-cut rotation in 25-year cycles. *EI* measures ecological similarity to simulated undisturbed old-growth forest, *YI* measures obtained yield (see section 5.2.5 *Assessment of logging scenarios* for details).

5.4 Discussion

The common usage of the term 'selective logging' refers to the more or less intensive commercial extraction of valuable timber species which is usually repeated after several decades. In contrast, we here studied the effects of continued low-intensity tree felling by the local population to meet their needs for fuelwood, and to provide fuelwood and charcoal for local markets. Apart from timber logging for sawmills, low-intensity selective logging is the main anthropogenic pressure on remaining fragments of old-growth cloud forest in central Veracruz, Mexico. Simulation results for different logging scenarios revealed that even at low intensity, selective logging severely alters forest structure and composition, and that those changes in some cases may only be detected after decades or even centuries of repeated disturbance.

5.4.1 Implications of "tala hormiga" for forest structure and composition

The most important impact of simulated low-intensity selective logging on forest structure was the dramatic loss of large old trees that are emerging over the main canopy of the forest. The number of small and medium-sized trees increased, and the forest became more homogeneous. When only selected species were cut (*S1* and *S2*), the change of forest structure was characterised by a sharp decrease of emergent trees > 80 cm dbh because the only emergent PFT was always a logging target. The species composition shifted towards non-logged species which accounted for an increase of the number of trees with 60 – 80 cm dbh.

As a result of the decline of emergent trees the size of gaps created either by natural treefall or logging is also expected to decrease. Already existing advance regeneration could benefit from decreasing gap sizes compared to pioneer species. Together with the higher frequency of gaps due to logging, this could account for the simulated stability of pioneer species. Field observations in the study area confirm both, the decrease of large old trees – in some forest fragments of the study area trees with a dbh > 60 cm are already lacking – and the fact that stem numbers of pioneer species do not increase significantly in disturbed fragments (G. Williams-Linera, pers. observation).

Okuda et al. (2003) studied forest structure and species composition in a regenerating lowland dipterocarp rain forest in Malaysia 41 years after the extraction of all trees ≥ 45 cm dbh. They found a significant increase of stem numbers of pioneer species and, similarly to our results, an increase of medium-sized trees. Similarly, Verburg and van Eijk-Bos (2003) observed an increase of pioneer species after logging in a Bornean rain forest. However, in both cases commercial logging accounted for a much higher removal of trees and associated damages than in our simulated scenarios. The decrease of gap sizes in regenerating and logged forests has been reported elsewhere (e.g. Chapman and Chapman 1997).

We assumed that maximum ingrowth rates of small trees at a dbh threshold of 1 cm are constant. The number of ingrowing saplings in the model is only modified by the light availability but does otherwise not respond to the disturbance regime. In reality, regeneration rates could be significantly altered in disturbed forest, e.g. by altered seed availability, seed predation, or microclimate. Thus, simulation results have to be interpreted keeping this restriction in mind. However, in cloud forest gaps in Costa Rica light availability was found to play an important role in determining densities of shade-tolerant and intolerant tree saplings (Lawton and Putz 1988). In our model, the number of ingrowing saplings was also not coupled to the species composition of the forest although seed production of a given species might decline due to the removal of mature trees. However, for oaks in oak-bamboo forest in Costa Rica it was observed, that smaller trees started earlier to reproduce and seed production increased after selective logging (Guariguata and Sáenz 2002). Likewise, abundant regeneration of climax species was found 20 years after an extraction of 15 – 46 m³/ha in lowland tropical rain forest in Suriname (Dekker and Graaf 2003).

Apart from the tree community, selective logging also has an impact on other taxa. There are many recent studies on the effects of selective logging on fauna and flora although most of them neglect the repetitive nature of logging by focusing on immediate or short-term effects after a logging operation. Contrasting responses of single taxa, guilds or diversity measures to selective logging have been reported including resilience (e.g. Costa and Magnusson 2002, Dunn 2004, Fredericksen and Fredericksen 2004, Holbech 2005), negative effects (e.g. Borgella and Gavin 2005, Dumbrell and Hill 2005) and positive effects (e.g. Lambert et al. 2005). However, the decline of the number of large old trees – and the associated decrease of standing dead trees and coarse woody debris – is likely to have a negative impact on many specialist plant and animal species that depend on them as habitat, food source, or nesting place. One good example is the study of Wolf (2005) who found that the diversity of epiphytes in Mexican pine-oak forest was negatively affected by the disappearance of large old trees.

LAI values of the entire forest stand differed only marginally from undisturbed old-growth forest. This may be explained by a rapid increase of LAI after disturbance with "overshooting" over the value of undisturbed old-growth forest. This pattern has been observed also in a field study by Hölscher et al. (2003) in montane oak forests in Costa Rica, and was confirmed by simulations of regenerating TMCF in the study area (Rüger et al. in press). Thus, ecosystem services provided by TMCF such as water capture from clouds and soil protection are not expected to decline when wood extraction does not exceed the regeneration capacity of the forest.

5.4.2 Recommendations for sustainable fuelwood extraction

Selective logging for fuelwood in natural old-growth forests will remain an important source of energy and income for the rural population in many tropical areas. If the ecological and environmental impacts of this forest use are to be kept to a minimum, certain precautionary measures should be considered. Logging should be extended to all canopy species to prevent major shifts in species composition of the forest. A certain number of large old trees should be maintained in the forest and allowed to grow and die naturally, especially when higher logging intensities are applied. Those trees make an important contribution to the maintenance of habitat for many specialist species, e.g. epiphytes and species that depend on dead wood (see above).

When all canopy species were targeted in our simulations and the minimum cutting diameter was 40 cm dbh, up to 12 m³/ha could be extracted annually from the forest. This rate may seem very high, but field data confirm that TMCF in central Veracruz reaches a basal area of 60 m²/ha within 80 years after the abandonment of cattle pasture (Muñiz-Castro et al. in press). Thus, if 60 m²/ha correspond to an overall wood volume of 500 – 600 m³/ha, the average rate of volume accumulation is 6 – 7.5 m³/ha per year, and maximum volume increment must be even higher. However, this intensive wood extraction was accompanied by a severe alteration of the structure and composition of the forest. The forest was artificially held in an intermediate stage of succession where trees were immediately cut when they exceeded a diameter of 40 cm. In cases where only species of intermediate shade tolerance are preferred for fuelwood use, it can be beneficial to cut also some large trees of shade-tolerant canopy species. In this way larger gaps are created that promote regeneration of less shade-tolerant species and possibly prevent the shift in species composition as observed in the respective logging scenarios. Similar recommendations for forest management are given in various studies that emphasise that large canopy openings are required to enhance regeneration of commercially valuable shade-intolerant tree species (e.g. Fredericksen and Putz 2003, and references therein).

The logging scenarios we compared in this study were sustainable *per definitionem*, because logging operations were omitted when the logging target could not be fulfilled. In reality however, people will change their strategy if they cannot meet their needs for fuelwood anymore. They will rather extend the range of logged species or switch to other tree sizes that were not preferred before. Additionally, it has to be taken into account, that simulation results regarding the yield of the different scenarios may be too optimistic due to the overestimation of biomass for large trees (> 50 cm dbh). Therefore, the investigated scenarios indicate the lower limit of ecological impact that a given logging scenario causes.

In the study area, the municipality of Tlalnelhuayocan has about 9.6 fuelwood users per ha of forest (Masera and Ghilardi, unpublished data). Assuming an intermediate annual fuelwood consumption of 675 kg per person (Ramírez-Bamonde 1996, Haeckel 2006), and an intermediate wood density of 0.6 g/cm^3, 1.1 m^3 fuelwood are consumed annually per person. This would result in an annual fuelwood need of about 11 m^3 per ha of forest. With the same data an average of 3.2 fuelwood users per ha of forest was estimated for the municipalities of Acatlán, Acajete, Chiconquiaco, and Naolinco. This corresponds to an annual fuelwood consumption of 3.6 m^3/ha. In these municipalities fuelwood extraction seems to be sustainable in terms of regeneration capacity of the forest, whereas it is at the limit of predicted productivity of the forest in Tlalnelhuayocan. Additionally, Tlalnelhuayocan borders the capital Xalapa where large amounts of fuelwood and charcoal are consumed by bakeries, restaurants, and inhabitants. This additional demand may drive extraction beyond sustainable limits. However, it is unclear, whether all the consumed wood in Xalapa comes from Tlalnelhuayocan or if it is complemented with wood from other sites. In a recent study, Haeckel (2006) predicts a rate of deforestation due to tree harvesting for fuelwood of 4.6 ha/y for the forests of the village Rancho Viejo in the municipality of Tlanelhuayocan.

For further simulation studies it would be desirable to incorporate more detailed socio-economic information regarding amounts of extracted wood, preferred tree species and sizes, to make the scenarios more realistic. Furthermore, we assumed that nutrient limitation is of minor importance both in the short term for species coexistence and in the long term for potential wood extraction. The nutrient rich volcanic soils of the study area legitimate this assumption. For other forest types growing on nutrient poor substrates, however, this assumption may not be valid.

In our study, ecological impact of the logging scenarios on the forest as measured by indices of structural and compositional change increased linearly with increasing wood extraction. This means that every additional amount of harvested wood always causes an additional change of forest structure and composition of the same magnitude. This emphasises the importance of priorities of the stake holders who have to decide how much alteration of the natural forests they are going to accept or how economic needs and ecological goals can be balanced. One possibility would be to intensify wood extraction in one portion of the forest while protecting another portion from human intervention (Fredericksen and Putz 2003).

Another alternative to relieve pressure on the remaining old-growth forest fragments could be the intensive management of secondary forest or the establishment of plantations of native tree species (McCrary et al. 2005). In the study area, forests regrowing after abandonment of agricultural fields or pastures are often dominated by species with intermediate shade tolerance and high growth rates (e.g. *C. caroliniana*, *L. styraciflua*). *L. styraciflua* has also been recommended for plantation culture by McCarter and Hughes (1984). Preliminary simulation results showed that a systematic management of secondary forest could provide yields of up to 12.5 m^3/ha per year. Management would include the prevention of regeneration of shade-tolerant species to promote the regeneration of the faster growing species with intermediate shade tolerance.

5.5 Conclusions

Forest models like FORMIND are useful tools to assess long-term implications of anthropogenic disturbance on forest ecosystems. Simulation results can support stake holders to design appropriate management strategies for natural species-rich forests, thus preventing the forests from undesired long-term degradation. Our study showed that repeated tree felling even at low intensity changes forest structure and composition in the long term. Ecological impact of wood extraction increases linearly with increasing levels of wood extraction. Forest structure becomes simplified and more homogeneous, because large old trees that emerge over the main canopy disappear from the forest. Species composition shifts to tree species that are not used for fuelwood. At least in some parts of the study region, fuelwood extraction seems to be at the limit of the regeneration capacity of the forest. In view of apparent forest exploitation at or even above sustainable limits and the increasing area of secondary forests, a deeper model-based analysis of a rational management of secondary forests seems to be worthwhile.

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SECONDARY TROPICAL MONTANE FORESTS: A SIMULATION STUDY OF THEIR POTENTIAL FOR PROVISION OF ECOSYSTEM SERVICES AND FUELWOOD*

Abstract

Secondary forests are increasing in area throughout the tropics. In central Veracruz, Mexico, the trend of deforestation has slowed down, and the area covered with secondary tropical montane cloud forest (TMCF) is increasing. Those secondary forests can play an important role in the provision of ecosystem services such as soil protection, water capture from clouds, conservation of native biodiversity, as well as goods such as fuelwood. We apply the process-based forest growth model FORMIND to study forest regeneration after abandonment of cattle pasture and to assess the potential for wood production of secondary TMCF in central Veracruz. We validate simulation results of forest regeneration by comparison with chronosequence data from the study region. The model predicted the qualitative development of aggregated forest characteristics correctly, although it slightly underestimated recovery time of the forest. We estimate that important structural forest characteristics for the ability of the forest to capture water and protect the soil such as forest height and leaf area index have recovered after 40 and 80 years at the latest. In contrast, forest properties which serve as indicators of the similarity of the species composition to old-growth conditions such as the number of large old trees and the proportion of basal area of the different PFTs need 150 and 300 years, respectively, to recover. A wood volume of up to 12.5 m^3/ha could be harvested annually from the forest. Thus, young secondary TMCF in central Veracruz can provide relevant ecosystem services, and rational management of the forest has the potential to substantially alleviate logging pressure on remaining old-growth forests.

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6.1 Introduction

By the end of the last century, there were 242 million ha of secondary forests in the tropics (Dupuy et al. 1999). Intensification of agriculture led to a decrease of prices of many crops and consequently to abandonment of marginal agricultural and grazing land (Aide and Grau 2004). On those abandoned lands, secondary forests are regrowing which provide important ecosystem services by preventing soil erosion, regulating regional water cycles, accumulating carbon, or harbouring native biodiversity. This raises the question as to how rates of desired ecosystem services vary during the course of succession, and how long it takes for a forest to recover those rates of old-growth forests (Guariguata and Ostertag 2001).

Secondary forests also have the potential to supply resources (e.g. timber and fuelwood) at a higher rate than old-growth forests due to their higher productivity, and offer an option for rational management. However, most research about management of tropical forests has concentrated on old-growth forests (but see Kammesheidt 2002, Kammesheidt et al. 2002). According to the UN Food and Agriculture Organization (FAO), secondary forests "represent one of the most serious challenges for forest managers and policy-makers. This is because so little is known about how to effectively manage these areas, particularly in tropical regions." (Dupuy et al. 1999).

In central Veracruz, the past five decades were characterised by accelerated conversion of primary tropical montane cloud forest (TMCF) into shade-coffee plantations, cattle pastures, agricultural fields, and urban areas (Williams-Linera et al. 2002). Only about 10 % of the original forest cover remained, mostly in small fragments. However, the decrease of undisturbed TMCF was accompanied by an increase of secondary forests (Manson et al. unpubl. manuscript), because land uses that became unprofitable were abandoned. These young secondary forests may provide ecosystem services considered of special importance in central Veracruz such as soil protection from erosion, especially on steep slopes, regulation of the water cycle, including flood prevention, water capture from clouds, and slow water release during the dry season (cf. Bruijnzeel 2004). Furthermore, central Veracruz belongs to the 25 biodiversity hotspots identified by Myers et al. (2000) and harbours a very diverse and highly endemic flora and fauna.

Many people in rural regions of central Veracruz depend on fuelwood from TMCF. An analysis of fuelwood consumption and availability in Mexico has classified most municipalities of the study area as medium to high priority areas, indicating high fuelwood use in these areas (Masera et al. 2004). Until now, there are almost no rationally managed second-growth forests in the study area, although population growth and deforestation have caused increased pressure on the few remaining old-growth forest fragments, and although young secondary forests are often dominated by species (e.g. *Liquidambar styraciflua*, *Carpinus caroliniana*) that are preferred for fuelwood (Challenger 1998, Haeckel 2006).

In this study, we apply the process-based forest growth model FORMIND (e.g. Köhler and Huth 1998, Köhler et al. 2001, Rüger et al. in press) to simulate the regeneration of TMCF in central Veracruz, Mexico, after abandonment of cattle pasture with respect to forest properties that are relevant for the provision of ecosystem services. Furthermore, we use the model to assess the potential of secondary TMCF for fuelwood production. The model is individual-tree-oriented and simulates the spatio-temporal dynamics of an uneven-aged mixed forest stand. FORMIND calculates the carbon balance for each individual tree on the basis of the light climate in the forest. The model has been parameterised for TMCF in central Veracruz on the basis of field data from the literature and the study site and expert judgments (Rüger et al. in press). We had the unique opportunity to directly test model predictions with field data from a chronosequence study of forest regeneration after abandonment of cattle pasture that has recently been carried out in the study region (Muñiz-Castro et al. in press). These data were not used during model development.

Thus, the objectives of this study are (1) to verify the ability of the model to project forest regeneration by comparing simulation results with chronosequence data, (2) to determine the recovery time of forest properties that are relevant to the ability of secondary TMCF to provide ecosystem services such as soil protection, water capture from clouds, and biodiversity conservation (e.g. leaf area index, forest height, forest structure, and forest composition in terms of plant functional types (PFT)), and (3) to assess the potential of secondary TMCF for fuelwood production.

Methods 6.2

Study area 6.2.1

TMCF in central Veracruz (19°30' N, 96°54' W), Mexico, occurs at an altitude between 1250 and 1875 m. The climate is mild and humid throughout the year. Annual precipitation varies between 1350 and 2200 mm; mean annual temperature is between 12 and 18°C (Williams-Linera 2002). The soil has been classified as Andosol (Rossignol 1987). The tree species that occur in the study area are grouped into plant functional types (PFTs). Criteria for classification into PFTs are light demand and maximum attainable height (Köhler et al. 2000). Three levels of shade tolerance are distinguished (shade-intolerant (i), intermediate (m), and shade-tolerant (t)). Three height groups are considered: small trees (≤ 15 m tall, ≤ 35 cm diameter at breast height (dbh)), canopy trees (≤ 25 m tall, ≤ 80 cm dbh), and emergent trees (≤ 35 m tall, ≤ 100 cm dbh). This classification results in six PFTs, because some of the combinations are rare (Table 6.1).

Table 6.1 Definition of plant functional types (PFTs) according to shade tolerance (T) and maximum attainable height (H_{max}). Three levels of shade tolerance are distinguished: i = shade-intolerant, m = intermediate, t = shade-tolerant. The successional status refers to the stage of succession in which a PFT attains maximum basal area values.

Plant functional type	PFT	T	H_{max}	Examples
Early successional small trees	1	i	15 m	*Heliocarpus*, *Myrsine*
Mid successional small trees	2	m	15 m	*Miconia*, *Oreopanax*
Late successional small trees	3	t	15 m	*Cinnamomum*, *Ilex*
Mid successional canopy trees	4	m	25 m	some *Quercus* spp.
Late successional canopy trees	5	t	25 m	*Magnolia*, *Beilschmiedia*
Emergents	6	m	35 m	*Liquidambar*, *Clethra*

Muñiz-Castro et al. (in press) studied the arboreous vegetation in 15 abandoned pastures ranging from a few months to 80 years in age. In each site, four 10 m × 10 m plots at a distance of 0 – 10 m and 40 – 50 m from the border with remaining old-growth forest were sampled. Basal area, density, mean height, and mean maximum height of individuals ≥ 5 cm dbh were calculated. For comparison with simulation results, we use only the data at a distance of 40 – 50 m from the forest border.

6.2.2 Model description

The individual-oriented forest growth model FORMIND simulates the spatial and temporal dynamics of uneven-aged mixed forest stands (e.g. Köhler and Huth 1998, Köhler 2000, Köhler et al. 2001, 2003, Huth et al. 2004, 2005). The model simulates a forest (in annual time steps) of several hectares as a mosaic of interacting grid cells with a size of 20 m × 20 m, corresponding to the crown size of large mature trees. It is assumed that light availability is the main driving force for individual tree growth and forest succession. Within each grid cell all trees compete for light and space following the gap model approach (Shugart 1998). For the explicit modelling of the competition for light each grid cell is divided into horizontal layers. In each height layer the leaf area is summed up and the light climate in the forest interior is calculated via an extinction law. The carbon balance of each individual tree is modelled explicitly, including the main physiological processes (photosynthesis, respiration) and litter fall. Growth process equations are modified from the models FORMIX3 and FORMIX3-Q (Ditzer et al. 2000, Huth and Ditzer 2000, 2001). Allometric functions relate above-ground biomass, stem diameter, tree height, crown diameter and stem volume. Tree mortality can occur either through self-thinning in densely populated grid cells, senescence, or gap formation by large falling trees. Gap formation links neighbouring grid cells. Regeneration rates are effective rates regarding the recruitment of small trees at a dbh threshold of 1 cm, with seed loss through predation and other processes already being implicitly incorporated.

Site conditions are assumed to be homogeneous and there is no inter-annual variability of climatic conditions in the model.

A detailed model description that follows the ODD protocol, which has been proposed as a standard protocol for describing individual- and agent-based models (Grimm and Railsback 2005, Grimm et al. in press), can be found in chapter 3. Details on model parameterisation for TMCF in central Veracruz are given in chapter 4. The mathematical formulation of biological processes and a table with model parameters are given in Appendix A of the thesis.

The ability of the model to reproduce observed forest characteristics of old-growth TMCF has been extensively tested (Rüger et al. in press). For single PFTs it was verified that simulated maximum diameter increment, stem numbers, basal area and diameter distributions matched field data. For the entire tree community it was checked that LAI, overall mortality rate as well as available light at forest floor correspond to field measurements (Table 6.2).

Table 6.2

Comparison of observed and simulated old-growth forest characteristics. Field observations mostly correspond to small areas (e.g. 0.1 ha), whereas simulation results are mean values for ten simulations (1 ha) and ten points in time.

Forest characteristics	Simulation	Observation	Reference
Total stem number[1]	1325 ind/ha	810 – 1700 ind/ha	Williams-Linera (2002)
Total basal area[1]	44 m^2/ha	35 – 89 m^2/ha	Williams-Linera (2002)
Mortality rate[1]	5.5%	1% – 12%	Williams-Linera (2002)
Available light on forest floor	10%	1% – 8.4%	Zuill and Lathrop (1975) Ramírez et al. (1998)
LAI	5	3.4 – 9.3	Hafkenscheid (2000), Fleischbein (2004)

[1] individuals ≥ 5 cm dbh

6.2.3 Simulation of forest regeneration

We simulate the regeneration of TMCF starting from a treeless area of 1 ha for 100 years. We assume that seed input is not limited, and that no further disturbances – other than gap creation by falling trees – occur during the course of succession. For comparison with field data, the simulation area is divided into plots of 10 m × 100 m. Mean and standard deviation of stem numbers, basal area, mean and maximum height for individuals ≥ 5 cm dbh are calculated. For simulation of long-term forest dynamics, 10 simulations are run for 1 ha and 400 years. Stem numbers and basal area of different PFTs, and stem numbers in different diameter classes are calculated.

6.2.4 Simulation of wood harvesting

Young secondary forests in the study area are dominated by tree species that belong to PFTs with intermediate shade tolerance (e.g. *Liquidambar styraciflua*, *Carpinus caroliniana*). Therefore, we simulate forest stands with only PFT 4, only PFT 6, or with PFT 4 and 6, in order to evaluate the potential of secondary TMCF for timber and fuelwood production. Simulations start from a treeless area of 9 ha and are run for 430 years. Selective logging starts after 38 years, when the first trees reach the minimum cutting diameter of 40 cm dbh. Logging takes place every year, and logging intensity is varied from 10 to 60 m^3/ha. If at a given time step the stem volume of all harvestable trees does not reach the volume value aimed at by the logging scenario, the respective logging operation is omitted. As wood extraction in the study area is carried out with the help of pack animals, logging damages are assumed to be low. Apart from trees that are killed by falling logged trees, 10% of the trees < 25 cm dbh are damaged. Larger trees are not affected by skidding damages. Felled trees are directed to already existing gaps if possible. Total harvest and number of omitted logging operations over the 430-year period are computed.

6.3 Results

6.3.1 Comparison of simulated forest regeneration with field observations

Model simulations of forest regeneration were compared to field data from abandoned pastures of different ages from the study region (Muñiz-Castro et al. in press). In general, simulated forest regeneration corresponded well with field data. Compared to the field data, the velocity of increase as well as maximum stem numbers were overestimated by the model during the first 20 years of succession (Fig. 6.1A). The simulated peak of stem numbers occurred after 10 years and amounted to approximately 3000 stems, whereas field data peaked after 23 years at a number of 2500 stems. In the longer run, simulated stem numbers corresponded well with field observations. Simulated basal area also increased faster than in the field data (Fig. 6.1B). The simulated peak of basal area occurred after 40 years, whereas the maximum in the field data was observed after 80 years. Both simulated and observed maximum basal area values were about 57 m^2/ha. Again, in the long term (100 years), field data fall in the range of simulated values. Stem numbers and basal area showed an “overshooting” during early and intermediate stages of succession, respectively. Mean tree height was predicted rather well by the model (Fig. 6.1C), whereas simulated maximum tree height was 4–7 m higher than in the field data, except for the first 10 years (Fig. 6.1D).

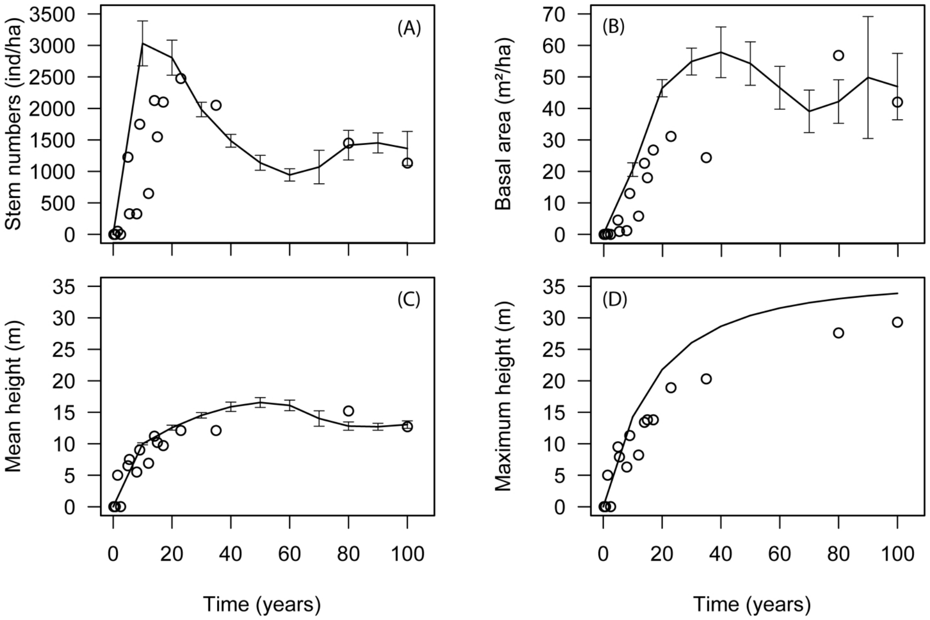

Figure 6.1

Simulation of forest regeneration from bare ground for 100 years. Stem numbers (A), basal area (B), mean height (C), and maximum height (D) are means of ten 10 m × 100 m plots (individuals ≥ 5 cm dbh). Standard deviation is shown for total stem numbers, basal area, and mean height. Circles are field data from 40 m × 100 m plots; the values at 100 years represent mature forest (Muñiz-Castro et al. in press).

Forest regeneration

6.3.2

Figure 6.2 shows the simulated course of succession over 400 years for the six PFTs. Both, total stem numbers (≥ 5 cm dbh) and total basal area reached their steady state after approximately 80 – 90 years. Simulated stem numbers leveled off at approximately 1350 ind/ha. The total basal area fluctuated around 44 m²/ha. During the first 20 years, all PFTs showed a peak of stem numbers. Pioneer species (PFT 1) accounted for most of the newly established individuals. Shade-tolerant PFTs (PFT 3 and 5) showed the lowest stem numbers. Self-thinning already started after 10 years, and stem numbers rapidly declined to their steady state values. In their steady state, pioneer species (PFT 1) were represented by only few individuals, because their establishment is possible only in canopy gaps.

During the first 20 years, pioneer species (PFT 1) accounted for most of the stand's basal area due to their fast growth. Then they were rapidly replaced by PFTs with intermediate shade tolerance (PFTs 2, 4, 6), which reached their maximum basal area after approximately 50 years. PFT 5, the slow-growing shade-tolerant canopy species, was the last in arriving at its steady state basal area after approximately 300 years. The increase in basal area of PFT 5 was accompanied by a decrease of PFTs 4 and 6.

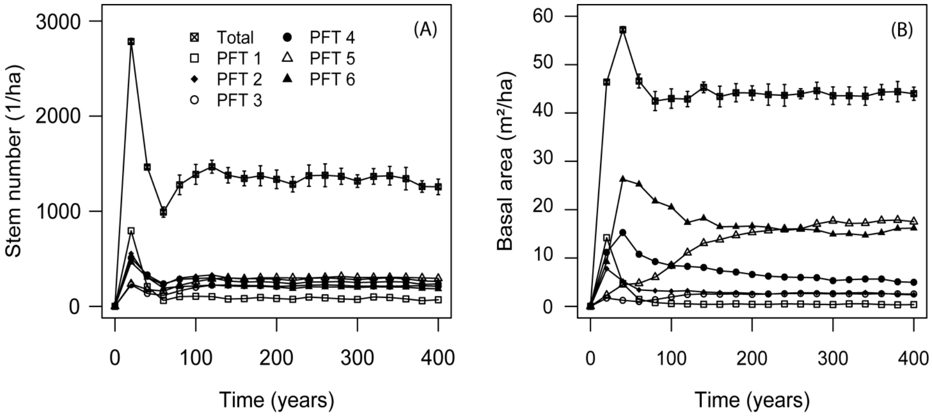

Figure 6.2 Simulation of forest regeneration from bare ground. Stem numbers (A) and basal area (B) are means of ten simulations for 1 ha and 400 years (individuals ≥ 5 cm dbh). Standard deviation is shown for total stem numbers and basal area.

It took 150 years until forest structure, measured as stem numbers in five diameter classes, reached equilibrium (Fig. 6.3). Trees > 60 cm dbh appeared first after 60 years, and trees > 80 cm dbh after 100 years.

LAI peaked 30 – 40 years after the beginning of succession, and then declined to about 4 after 70 years (Fig. 6.4).

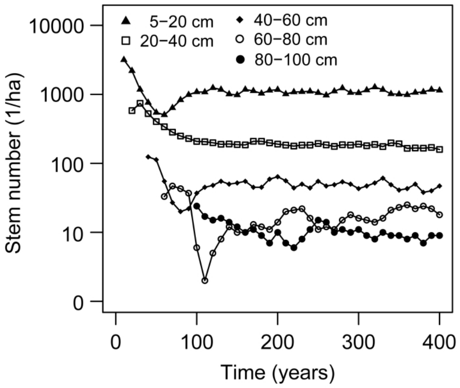

Figure 6.3 Stem numbers in five diameter classes during forest regeneration from bare ground. Simulations were run for 1 ha and 400 years.

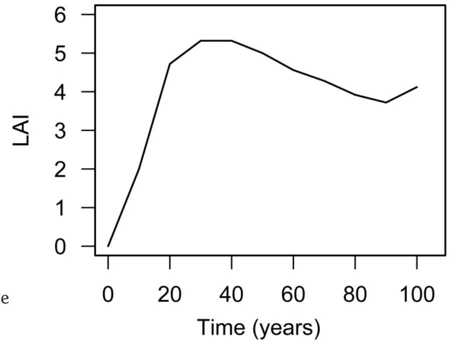

Figure 6.4

Recovery of leaf area index (LAI) during the first 100 years of forest regeneration.

6.3.3 Wood harvesting

Total harvest over the 430 year period was very similar for secondary forests exclusively composed of PFT 4, PFT 6, and PFTs 4 and 6 (Fig. 6.5). Maximum total harvest reached about 5000 m^3/ha, when the logging target was 60 m^3/ha. Translated to an annual basis, mean annual volume increment was up to 12.5 m^3/ha. The mixed forest was slightly more productive than the stands dominated by only one PFT. When the logging target for every logging operation increased, the percentage of omitted logging operations also increased, i.e. the time between two harvests had to be extended. If high amounts of wood volume were to be harvested (60 m^3/ha), logging could only take place approximately every fifth year. This had a positive effect on total harvest, because part of the logging damages was considered to be independent from logging intensity. Therefore, highest harvests were achieved when high amounts of wood were cut at relatively long intervals.

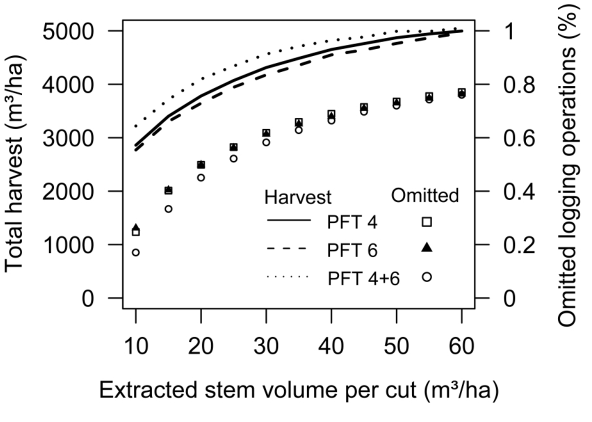

Figure 6.5

Total harvest over 430 years and percentage of omitted logging operations for selectively logged secondary TMCF (composed of PFT 4, PFT 6, PFT 4+6) when different logging intensities are simulated. Simulations were run for 9 ha and 430 years.

6.4 Discussion

6.4.1 Ability of the model to predict forest regeneration

There are few forest models that simulate the succession of species-rich tropical forests and it is even rarer that chronosequence data from the same study site are available that enable a model validation with independent data (but see Moorcroft et al. 2001). The model predicted the qualitative development of aggregated forest characteristics correctly. Compared to the field data, the model overestimated the speed of forest recovery. During the first 10 years, differences between model simulations and field observations were due to the higher number of trees in the model. After that, the trees in the model seemed to grow slightly faster than in reality, because stem numbers were predicted correctly, whereas basal area and maximum height were overestimated. Unfortunately, there are no data available for secondary forests of intermediate ages, i.e. between 35 and 80 years.

Taking into account that the model was calibrated such that old-growth forest characteristics were reproduced, our results emphasise the ability of process-based forest models to predict forest dynamics on the basis of included processes (i.e. recruitment, tree growth, mortality, competition for light and space, and gap creation by falling trees). To calibrate model parameters for which no field data were available, we used various sources of other information, e.g. data on diameter increment to determine respiration parameters and data on old-growth forest structure and composition to adjust recruitment and mortality rates of the different PFTs (Rüger et al. in press). This pattern-oriented modelling approach assured that the processes that occur in reality are well represented by the model (e.g. Grimm et al. 2005).

As recruitment rates were adjusted to old-growth forest conditions, they reflect regeneration after gap creation or under a closed forest canopy, and processes that may become important in open areas such as competition with non-arboreous vegetation, increased mortality due to desiccation, and limited seed dispersal were neglected. The data of Muñiz-Castro et al. (in press), however, were sampled on abandoned pastures where native grasses dominated at the time of abandonment. This may be an explanation for the slightly overestimated stem numbers during the first years of succession. Thus, the model can be regarded to simulate an “ideal case”, i.e. succession from bare ground without limitation of seed input or competition with vegetation that established during previous land use.

6.4.2 Recovery time of relevant forest properties for the provision of ecosystem services

LAI and maximum height of the forest are two forest properties that are important for the provision of ecosystem services such as water capture and soil protection (Challenger 1998). According to simulation results and field data, LAI recovered after 20 years and forest height reached ²⁄₃ of an old-growth forest after 40 years. Taking into account the overestimation of succession speed, we assume that secondary TMCF of 40 years provide these ecosystem services at least to a large extend as compared to mature forest. The pattern of ‘overshooting’ of LAI values has also been reported by Hölscher et al. (2003), who found significantly higher LAI values in 40-year old secondary upper montane rain forest in Costa Rica than in old-growth forest. The predicted peak of basal area at intermediate stages of succession was only observed in one out of six chronosequence studies in the Neotropics (Guariguata and Ostertag 2001, and references therein).

Two forest properties that serve as indicators of the similarity of the species composition to old-growth conditions are the number of large old trees and the proportion of basal area of the different PFTs. Both properties need a long time to recover. Our results suggest that the basal area of the different PFTs continues to change until 300 years after the beginning of succession. This result is confirmed by chronosequence studies in the Neotropics where it was found that the canopy composition after 80 – 100 years was still not similar to old-growth forest (Saldarriaga et al. 1988, Denslow and Guzman 2000). In the simulations, it takes 150 years until the number of large trees resembles that of old-growth forests. However, until the number of senescent trees and the amount of dead woody debris reach values of an old-growth forest, much more time might elapse. Clearly, many plant and animal species depend on large trees, old trees or dead woody debris (e.g. epiphytes, insects, birds), and species with very specific habitat requirements and limited dispersal abilities might never be able to establish in fragments of secondary forest surrounded by a non-forest matrix. Thus, our simulation results confirm the conclusion of Guariguata and Ostertag (2001) that many structural and functional characteristics recover rapidly, whereas the species composition of the forest needs a much longer time span to resemble that of old-growth conditions.

Potential of secondary forests for wood production 6.4.3

The individual-based and process-based modelling approach enabled us to simulate wood extraction from secondary forests dominated by tree species with an intermediate shade tolerance. The simulated managed secondary forests were artificially held at an intermediate successional stage corresponding to a 40-year old forest with maximum diameters slightly above 40 cm by logging larger trees and by preventing regeneration of pioneer and shade-tolerant species.

Results show that up to 12.5 m³/ha can be harvested from the forest every year. Taking into account that the model seems to slightly overestimate tree growth this result has to be interpreted with caution. However, field data confirm that TMCF in central Veracruz reaches a basal area of 25 m²/ha within 20 years after the abandonment of cattle pasture and 60 m²/ha within 80 years (Muñiz-Castro et al. in press). If 25 m²/ha roughly correspond to an overall wood volume of 200 – 300 m³/ha, and 60 m²/ha to 500 – 600 m³/ha, then average volume increment for the first 20 years of succession is 12.5 – 15 m³/ha per year, and 6 – 7.5 m³/ha per year for the first 80 years. Thus, simulation results may lie in a realistic range. However, additional data on diameter increment especially of species with intermediate shade tolerance under different competition situations could help to improve the model parameterisation.

A rational management could optimise yields by choosing an appropriate felling diameter or by applying additional silvicultural practices such as thinning. Against these considerations, simulated forest productivity should be regarded as a rough indication of the potential of secondary TMCF for wood extraction rather than a specific management recommendation. However, 12.5 m³/ha per year is a large quantity, especially if compared to the mean annual yield of Mexican forests, which is estimated to be 1.2 m³/ha per year

(Torres-Rojo 2004). Productivity of Mexican TMCF is also higher than that of untreated secondary tropical lowland humid forests which ranges between 1 – 9 m^3/ha per year. This may be due to the higher soil fertility of the volcanic soils in the study region. However, productivity was lower than that of single-species plantations of teak (5 – 20 m^3/ha per year) and melina (13 – 30 m^3/ha per year) (Kammesheidt 2002, and references therein).

The slightly higher productivity of the simulated forest with two PFTs compared to simulations with only one PFT may be due to complementary resource exploitation when trees with different ecological characteristics are present (e.g. Fridley 2003). The two PFTs that we simulated together do not differ in their ability to exploit light, but perhaps they are complementary in space partitioning. In other studies the productivity of a mixed forest was between the productivities of the monocultures (e.g. Bartelink 2000).

6.5 Conclusions

We conclude that structural properties such as forest height, basal area, and leaf area of secondary TMCF in central Veracruz recover rapidly. Especially, its potential to capture water from the clouds and to protect the soil from erosion is expected to have recovered after 40 years of regeneration at the latest. However, other forest properties that play an important role for the diversity of plant and animal species that are adapted to old-growth forests such as the number of large and senescent trees as well as the share of shade-tolerant canopy species need several hundred years to resemble that of mature forests. Secondary TMCF has a very high potential for production of fuelwood which is presently harvested in remaining old-growth forest fragments in central Veracruz. Therefore, intensive wood extraction from the young secondary forests could satisfy the needs for fuelwood of the rural population, while at the same time minimising anthropogenic disturbance of the remaining old-growth TMCF fragments and contributing to the conservation of their immense species diversity.

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IDENTIFYING ECOLOGICAL IMPACTS OF POTENTIAL HARVESTING STRATEGIES FOR TEMPERATE EVERGREEN RAIN FOREST IN SOUTHERN CHILE – A SIMULATION EXPERIMENT*

Abstract

Current forestry practices in southern Chile largely rely on the management of exotic tree plantations following clear-cutting of native forests. Few experiences exist on silvicultural management of species-rich native evergreen rain forests. Nevertheless, conservationists and forest scientists call for sustainable management of native forests as a way to conserve their highly endemic biodiversity and to protect ecosystem services. Here, we applied the process-based forest growth model FORMIND to compare different harvesting strategies in regard to potential harvest and ecological impacts. FORMIND is individual-tree-oriented and simulates the spatio-temporal dynamics of an uneven-aged mixed forest stand. For each tree species we defined model parameters related to regeneration, growth, and mortality. We tested the model by comparing simulation results with inventory data and other field observations from an old-growth Valdivian temperate rain forest (VTRF) from Guabún, northern Chiloé Island. We simulated different logging practices such as selective logging and clear-cutting in narrow bands to investigate their long-term impact on forest structure and composition.

Results showed that up to 13 m³/ha per year could be harvested when logging in bands was applied because it promotes the regeneration of the relatively light-demanding and fast-growing *Eucryphia cordifolia*. However, forest structure and composition are severely altered by logging in bands. In contrast, selective logging provides lower harvests but better conserves old-growth forest characteristics. Logging gaps created by selective logging are not large enough to assure regeneration of *E. cordifolia*, but favour shade-tolerant species such as *Laureliopsis philippiana*. We recommend leaving some large, canopy-emergent old trees in the forest stand since most logging scenarios failed to keep them. Our simulation results provide relevant guidelines for sustainable management of VTRF, thereby providing opportunities for the conservation and use of native biodiversity outside protected areas.

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* A slightly modified version of this chapter is intended for publication as Rüger, N., A. G. Gutiérrez, W. D. Kissling, J. J. Armesto, and A. Huth. “Identifying ecological impacts of potential harvesting strategies for temperate evergreen rain forest in southern Chile – a simulation experiment” in a journal of forest ecology or applied ecology.

7.1 Introduction

Temperate evergreen rain forests cover more than 40,000 km^2 along the western margin of southern South America, restricted mainly to lowland and mid-elevation areas (Donoso 1998, CONAF-CONAMA 1999). These forests occur in one of the 25 biodiversity hotspots identified by Myers et al. (2000) and the Valdivian forest subtype has been classified among the 200 biologically most valuable and critically endangered ecoregions of the world (Olson and Dinerstein 1998). Southern temperate forests are severely threatened by land conversion to grassland or to monospecific plantations of *Pinus radiata* or *Eucalyptus* species.

Exotic tree plantations increased substantially since 1974, when the Chilean Government provided a subsidy to defer the cost of planting and subsequent management (Lara and Veblen 1993, Donoso and Lara 1999). Today conifer and eucalyptus plantations cover nearly 3 million hectares and sustain more than 95% of the internal and foreign markets for timber and wood pulp in Chile. However, Chilean foresters, biologists, and agronomists have called for changes to the forestry legislation to foster the sustainable management of remaining native forests as a way to protect wildlife habitats and maintain the valuable ecological services that these forests provide (Lara et al. 2003). Native forests deliver clean water for human use as well as for salmon breeding and fishing, timber, fuelwood, and non-timber forest products to local communities. Native forests have cultural, religious, and recreation values in addition to harbour a large fraction of native biodiversity (Lara et al. 2003). Southern rain forests contain a high number of endemic flora and fauna because of their long biogeographic isolation in the western margin of the continent (Aravena 1991, Galloway et al. 1996, Armesto et al. 1999a, Muñoz et al. 2003).

While largely monospecific stands of *Nothofagus pumilio* and *Nothofagus betuloides* at higher latitudes (45 – 55° S) offer promising perspectives for sustainable timber harvest (Armesto et al. 1996, Arroyo et al. 1999b), it is doubted whether Valdivian temperate rain forest (VTRF, Veblen et al. 1983) can be managed for timber production in an ecologically sustainable and, at the same time, economically feasible way (e.g. Arroyo et al. 1999a). These doubts arise from the higher structural complexity and tree species richness of Valdivian rain forest, and its stronger dependence on mutualistic biotic interactions for pollination and seed dispersal (Armesto et al. 1996, Smith-Ramírez et al. 2005a).

During recent decades, pilot silvicultural experiments have been initiated to explore the potential for timber extraction from evergreen rain forests and to assess tree regeneration after different silvicultural treatments (e.g. Donoso 1989b, CONAF-CONAMA 1999, Lara et al. 2000). However, the design, execution, and monitoring of large silvicultural experiments are costly and operationally difficult (Armesto et al. 1999c). Thus, modelling approaches which are complementary to experimental studies are needed to assess the long-term consequences of different management options and to provide guidelines for forest managers and planners aiming at reconciling conservation and production objectives (Lindenmayer and Franklin 2002).

Here, we apply the process-based forest growth model FORMIND (e.g. Köhler and Huth 1998, Köhler et al. 2001) to compare different harvesting strategies and to assess the potential of different management options that reconcile timber production with long-term maintenance of forest structure and composition (Franklin 1993, Armesto et al. 1998). FORMIND is individual-oriented and calculates the carbon balance for each individual tree on the basis of the light environment in the forest. Hence, the model allows for the detailed incorporation of different logging strategies. To our knowledge, this is the first study that analyses timber harvesting options for Chilean evergreen rain forests by applying a process-based simulation model.

Currently, many native old-growth forests in southern Chile are “creamed”, i.e. the most valuable trees are selectively harvested leaving unhealthy, senescent, twisted, and small trees behind. In a first logging scenario, we try to investigate long-term consequences of this practice. Cutting is restricted to the diameter range between 50 and 100 cm, whereas larger trees remain in the forest. In a second scenario, we simulate the same type of selective logging of large trees, but removing all trees with diameters > 1 m prior to management to explore potential positive effects of this practice on forest productivity. In a third scenario, we simulate clear-cutting in narrow strips because this treatment should promote the regeneration of dominant tree species after harvesting Valdivian evergreen rain forests (Donoso 1989b). Large-scale clear-cutting is not a suitable silvicultural treatment for VTRF due to problems of soil erosion, nutrient losses, biodiversity conservation, and tree regeneration requirements, and we therefore do not simulate large-scale clear-cutting scenarios (Donoso 1989b, Armesto et al. 1999b, c). We suggest that our simulation results can provide guidelines for future sustainable management, thereby providing opportunities for the conservation and use of native biodiversity outside protected areas (Franklin 1993, Armesto et al. 1998).

7.2 Methods

7.2.1 Study area

The study site was a large remnant (200 ha) of Valdivian evergreen forest located in Guabún, Chiloé Island, Chile (41°50'S), about 30 km northwest of Ancud (Fig. 7.1). The prevailing climate is wet-temperate with strong oceanic influence (Di Castri and Hajek 1976). Rainfall occurs throughout the year. The nearest meteorological station in Punta Corona (41°47'S, 73°52'W) has an annual average of 2444 mm of rainfall and a mean annual temperature of 10.7°C. Mean maximum and minimum monthly temperatures are 13.8°C (January) and 8.3°C (July).

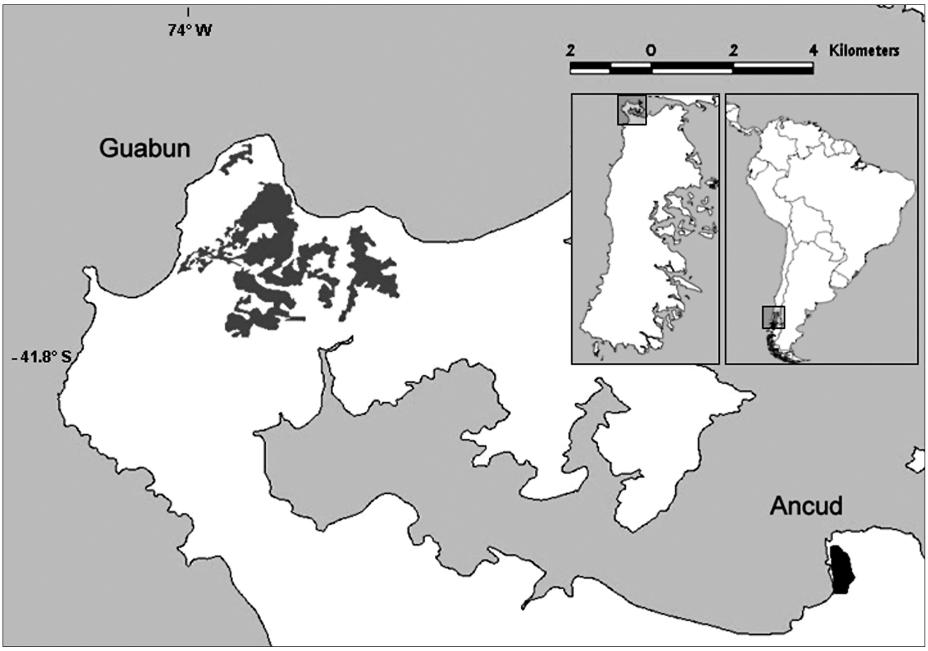


Figure 7.1 Location of the study area Guabún in northern Chiloé Island, Chile. Old-growth forests are shown in grey.

Inventories were conducted in a coastal remnant of old-growth Valdivian temperate rain forest (VTRF). Floristically, this forest type is dominated by *Eucryphia cordifolia* (Eucryphiaceae), *Aextoxicon punctatum* (only member of the endemic Aextoxicaceae), and *Laureliopsis philippiana* (Monimiaceae). In addition, several myrtaceous tree species occur mostly in the lower canopy. This forest stand was selected for study because from dendrochronological data of oldest cohorts there was no evidence of catastrophic disturbance, such as fire or stand-scale logging for at least 400 years (Gutiérrez et al., unpubl. manuscript). Stand structure and composition are similar to old-growth VTRF stands in Chiloé Island and mainland sites in the Chilean Lake District (Donoso et al. 1984, 1985, Veblen 1985, Donoso 2002).

Model tree species 7.2.2

The model focused on three canopy-dominant tree species and one sub-canopy species group. *Eucryphia cordifolia* is a canopy-emergent species (up to 40 m in height and 2 m in diameter). It is considered light-demanding and requires medium to large-scale disturbances for establishment (Veblen 1985, Donoso et al. 1985). *Aextoxicon punctatum* and *Laureliopsis philippiana* are both shade-tolerant species occurring in the main canopy of the forest. They reach heights of 30 m and diameters of up to 1 m. Several tree species in the Myrtaceae family (*Amomyrtus luma*, *A. meli*, *Luma apiculata*, *Myrceugenia ovata*, *M. planipes*) are grouped into one plant functional type (PFT) because of their similar ecological characteristics. They are all shade-tolerant and with maximum heights of 15 – 20 m they often dominate the lower canopy. A few other tree species (e.g. *Drimys winteri*, *Pseudopanax laetevirens*) occur at the study site, but they are relatively rare and were not included in our simulations.

The process-based forest growth model FORMIND 7.2.3

The individual-oriented forest growth model FORMIND simulates the spatial and temporal dynamics of uneven-aged mixed forest stands (e.g. Köhler and Huth 1998, Köhler 2000, Köhler et al. 2001, 2003, Huth et al. 2004, 2005). The model simulates a forest (in annual time steps) of several hectares as a mosaic of interacting grid cells with a size of 20 m × 20 m, corresponding to the crown size of large mature trees. It is assumed that light availability is the main driving force for individual tree growth and forest succession. Within each grid cell all trees compete for light and space following the gap model approach (Shugart 1998). For the explicit modelling of the competition for light each grid cell is divided into horizontal layers. In each height layer the leaf area is summed up and the light climate in the forest interior is calculated via an extinction law. The carbon balance of each individual tree is modelled explicitly, including the main physiological processes (photosynthesis, respiration) and litter fall. Growth process equations are modified from the models FORMIX3 and FORMIX3-Q (Ditzer et al. 2000, Huth and Ditzer 2000, 2001). Allometric functions relate above-ground biomass, stem diameter, tree height, crown diameter, and stem volume. Tree mortality can occur either through self-thinning in densely populated grid cells, senescence, gap formation by large falling trees, or medium-scale windthrows (800 – 1600 m²), which occur in the study area (Veblen 1985, A. Gutiérrez, pers. observation). Gap formation links neighbouring grid cells. Regeneration rates are effective rates regarding the recruitment of small trees at a diameter at breast height (dbh) threshold of 1 cm, with seed loss through predation and other processes already being implicitly incorporated. Site conditions are assumed to be homogeneous and there is no inter-annual variability of climatic conditions in the model.

FORMIND has been parameterised for VTRF, particularly coastal stands in Chiloé Island. However, similar stands dominated by *Eucryphia*, *Aextoxicon*, *Laureliopsis*, and myrtaceous species are widespread in the Coastal Range on the mainland (Smith-Ramírez et al. 2005b). A detailed model description that follows the ODD protocol, which has been proposed as a standard protocol for describing individual- and agent-based models (Grimm and Railsback 2005), can be found in Grimm et al. (in press). A table with model parameters is given in Appendix A of this thesis.

To assess the long-term dynamics of the forest following natural large-scale disturbance, we started from a treeless area which is regarded to be suitable for the establishment of all species. For the logging scenarios, we used inventory data from the study site as initial condition. Inventory data for 0.4 ha old-growth forest (see below) were expanded to an area of 9 ha and individual trees were randomly distributed among the grid cells.

7.2.4 Model evaluation

To test the ability of the model to reproduce observed forest characteristics, we compared simulation results with field data at different levels. At the level of individual trees, we compared simulated and measured diameter increment and stem volume values. At the species-level, we compared inventory data of the old-growth forest with the simulated forest 400 years after a large-scale disturbance.

Inventory data consist of six transects (together 4000 m²) within a forest stand that has not been affected by large-scale disturbances for at least 400 years (Gutiérrez et al., unpubl. manuscript). All trees > 5 cm dbh were measured and their species identified. To estimate radial growth, 47 randomly located trees were cored and cores were analysed with standard dendrochronological techniques (Gutiérrez et al., unpubl. manuscript). Diameter increment was approximated by multiplying tree ring width by 2. Simulations of maximum diameter increment were carried out for a single tree of each species under full sunlight conditions.

To assess the reliability of stem volume values calculated by FORMIND, we compared them to empirical volume functions for the different species (Emanuelli and Pancel 1999, Salas 2002).

We simulated forest regeneration over 1500 years with and without natural medium-scale disturbances to study forest succession and the dependence of the maintenance of current forest composition on natural medium-scale disturbances. Ten simulations were carried out for a simulation area of 1 ha, and averages and standard deviations were calculated for stem numbers and basal area of the different species.

An extensive sensitivity analysis was carried out to explore the impact of model parameters on model outcomes. Details on methods and results of this sensitivity analysis are given in the Appendix of this chapter.

Implementation of logging scenarios 7.2.5

We selected three logging strategies (selective logging with and without remaining large old trees, logging in bands), which either resemble current logging practices or which have been suggested as suitable options for management of VTRF (Donoso 1989b, Armesto et al. 1999c). Within each strategy, different scenarios were simulated which varied the harvested stem volume and logging cycle (in the case of selective logging) and the logging cycle (in the case of band logging). The model was initialised with inventory data from an old-growth forest stand. Logging operations were repeated over 400 years.

Selective logging – Selective logging in this case refers to the selective logging of trees with a dbh of 50 – 100 cm. Our two selective logging strategies differ in the way large old and probably senescent trees are treated. In the first case (with large trees), trees > 1 m dbh are left standing, because they often exhibit heart rot and do not provide valuable timber. In the second case (without large trees), all trees > 1 m dbh are removed prior to the simulation of logging scenarios to enhance growth of potential future crop trees by reducing competition.

We varied the time between two sequential harvesting operations (logging cycle) from 10 to 50 years. For each logging cycle we varied the harvested stem volume (harvest aim) such that on an annual basis 1 – 10 m³/ha were harvested. For a logging cycle of 10 years this corresponds to harvesting 10 – 100 m³/ha, and for a logging cycle of 50 years to 50 – 500 m³/ha. In the case when the harvestable volume is lower than the harvest aim, the logging operation was omitted. Within the diameter range of 50 – 100 cm, the largest trees were always logged first.

Logging damage to the remaining trees was divided into direct damage by the falling tree and additional damage due to skidding. We assumed reduced-impact logging where falling trees are directed to existing gaps if possible. No damage occurred to trees > 50 cm dbh. Skidding damages were assumed to increase with increasing levels of wood extraction (Fig. 7.2).

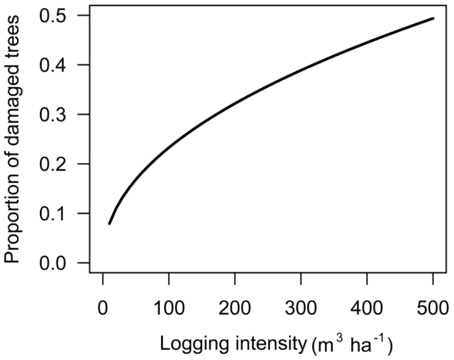


Figure 7.2 Proportion of damaged trees due to skidding operations assumed in model simulations.

Logging in bands – Logging in bands was simulated with clear-cutting in 20 m wide bands. Thus, the size of the created gap was 0.2 ha per ha. The return time to each band was varied from 50 to 150 years. Skidding damage was considered to be only 10 %, because logging bands can be used to extract trees from the forest. No damage occurred to trees > 50 cm dbh.

7.2.6 Assessment of logging scenarios

To evaluate the economic and ecological implications of a given logging scenario we calculated four variables, namely total harvest (*H*), an index of structural change (*ISC*), an index of compositional change (*ICC*), and leaf area index (*LAI*). *H* is an economic indicator of timber harvest, *ISC* and *ICC* are ecological indicators of changes in forest structure and species composition, and *LAI* is an environmental indicator of erosion risk in this high rainfall region.

H was calculated for each scenario over the simulation period of 400 years. *ISC* was calculated as

$$ISC = \frac{1}{3}\sum_{i=1}^{3}\frac{|\bar{x}_{s_i} - \bar{x}_{c_i}|}{\bar{x}_{c_i}},$$

i.e., the difference in mean numbers of trees (time steps 300 – 400) in three different diameter classes ($\bar{x}_{s_i}$, s_1: 5 – 50 cm, s_2: 50 – 100 cm, and s_3: > 100 cm dbh) of a simulated logged forest in comparison to a simulated control forest ($\bar{x}_{c_i}$, $i = 1 – 3$) where no logging had been applied. *ICC* indicates the change in relative importance of tree species of the logged forest in relation to an unlogged control forest based on importance values (*IV*). Importance values of the different species (*i*) were calculated as

$$IV_i = \frac{1}{2}\left(\frac{ba_i}{ba_{total}} + \frac{n_i}{n_{total}}\right),$$

i.e., the sum of relative basal area (*ba*, m²/ha) and relative density (*n*, trees/ha) of the focal species in relation to all species (*total*). *ICC* was calculated for the last 100 years of the simulation (time steps 300 – 400) as

$$ICC = \frac{1}{4}\sum_{i=1}^{4}\frac{\left|\overline{IV}_{s_i} - \overline{IV}_{c_i}\right|}{\overline{IV}_{c_i}},$$

i.e., summing the differences between mean *IV* of species *i* in the logging scenario ($\overline{IV}_{s_i}$) and the unlogged control forest ($\overline{IV}_{c_i}$) relative to its mean *IV* in the control forest (species are *A. punctatum*, *E. cordifolia*, *L. philippiana*, and Myrtaceae). *LAI* values were directly determined from model output and averaged over time steps 300 – 400.

To contrast economic benefit and ecological impact of a logging scenario, we calculated an ecological index (*EI*), which measures the similarity of a logged forest to undisturbed old-growth forest. *EI* includes the ecological variables *ISC*, *ICC*, and *LAI*, and the number of old trees (> 1 m dbh, *OLD*) which were divided by the maximum value obtained from all logging scenarios (ISC_{max}, ICC_{max}, LAI_{max}, OLD_{max}) and summed up:

$$EI = \frac{1}{4}\left(\left(1 - \frac{ISC}{ISC_{max}}\right) + \left(1 - \frac{ICC}{ICC_{max}}\right) + \frac{LAI}{LAI_{max}} + \frac{OLD}{OLD_{max}}\right).$$

For comparison, we evaluated *EI* for simulated undisturbed old-growth forest, bare ground, and a fictitious *Eucalyptus* plantation. For bare ground, *LAI* and *OLD* are 0, whereas *ISC* and *ICC* are 1. For the *Eucalyptus* plantation we assumed a mean annual volume increment of 22 m³/ha and *LAI* of 3. We assumed that all stems are in the smallest diameter class (5 – 50 cm), and assumed the stem number per hectare to be 625. From these assumptions results an *ISC* of 0.88. *OLD* is 0. *ICC* can not be calculated with our index formula, because *Eucalyptus* does not exist in the native forest, and *ICC* would theoretically be infinite if another term would be added to the index. However, for practical reasons, we assumed *ICC* to be 2.

Results 7.3

Model evaluation 7.3.1

Diameter increment – Simulated maximum annual diameter increment (SMDI) and empirical diameter increment values (A. Gutiérrez, unpubl. data) are shown for all species in Figure 7.3. SMDI of *A. punctatum* corresponded well with maxima of observed values. Measurements above the SMDI are attributed to especially favourable weather conditions or measurement errors. For *E. cordifolia* SMDI matched well with maximum values measured for small diameters. For intermediate diameters SMDI was lower than maxima of field observations. For large diameters no field data were available. For *L. philippiana* SMDI corresponded well with maximum observed values. No field data were available for myrtaceous species at the study site. However, SMDI of 6 mm/y compared well with measured maximum diameter increment of 6.2 mm/y (maximum radial increment was 3.1 mm/y) from Puyehue National Park in the Andean Range, Chile (Pollmann and Veblen, unpubl. data).

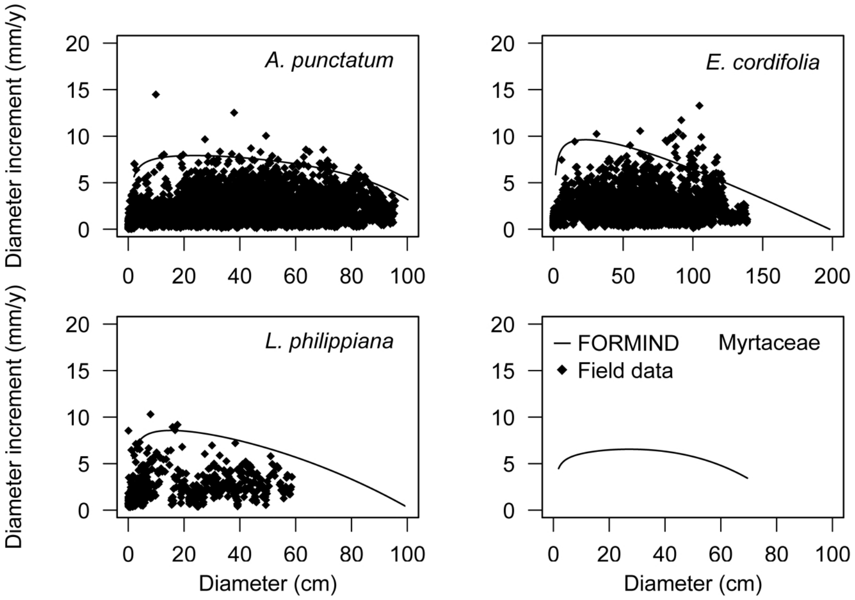


Figure 7.3 Simulated (lines) and measured (dots) annual diameter increment. Simulations were carried out under full light conditions (700 µmol(photons)·m^{-2}s^{-1}) and represent maximum potential growth. Field data are derived from radial growth measurements (Gutiérrez et al., unpubl. manuscript).

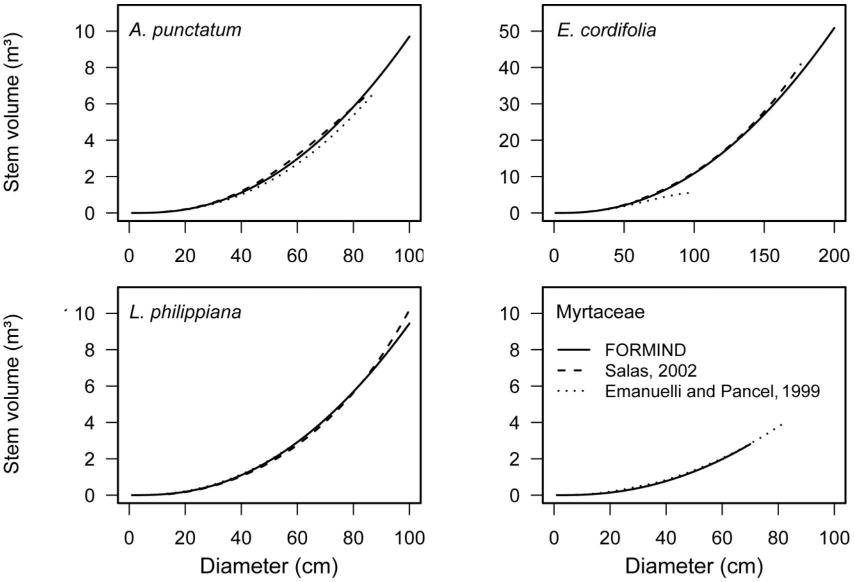


Figure 7.4 Stem volume of single trees calculated with FORMIND and empirical volume functions from Emanuelli and Pancel (1999) and Salas (2002).

Stem volume – For all species, stem volume values calculated by FORMIND corresponded well with empirical volume functions (Emanuelli and Pancel 1999, Salas 2002; Fig. 7.4).

Simulation of long-term forest dynamics – The simulation of long-term forest dynamics over a 1500 year period without medium and large external disturbances (e.g. multiple-tree wind throws) is shown in Figure 7.5 (A, B). Total tree density reached its long-term steady state within the first 100 years (Fig. 7.5A). *E. cordifolia* tended to disappear from the forest after approximately 800 years. *A. punctatum* stabilised at relatively low density, *L. philippiana* at intermediate density, and the myrtaceous species reached high densities. In terms of basal area, the first 400 years of succession were dominated by *E. cordifolia*, which was then replaced by the shade-tolerant species (Fig. 7.5B). Myrtaceae accounted for the highest basal area, followed by *L. philippiana* and *A. punctatum*.

According to field data, the study site has not been affected by disturbances other than single tree falls for around 400 years (Gutiérrez et al., unpubl. manuscript). Consequently, the simulated forest can be compared to the inventory data 400 years after the initiation of the succession. The symbols in the grey bars on the right side of each chart of Figure 7.5 represent inventory data from the study site. Simulated stem numbers and basal area of the different species after 400 years (grey bars) correspond reasonably well with inventory data, suggesting that the main trends of forest dynamics are captured in our model.

Incorporating natural medium-scale disturbances into the model changes long-term forest dynamics and is similar to simulating a larger spatial scale where forest patches in different successional stages occur side by side. Again, total stem numbers and total basal area reached a steady state after approximately 100 – 200 years (Fig. 7.5C, D). Simulated stem numbers levelled off at about 1950 trees/ha. Total basal area reached 95 m^2/ha. At the beginning of stand regeneration, the forest was dominated by myrtaceous species in terms of stem numbers and by *E. cordifolia* in terms of basal area. Stem numbers reached a steady state already after 100 years, whereas basal areas of the four species continued to change for about 1000 years. Again, the main trend was the replacement of *E. cordifolia* by shade-tolerant species. In contrast to forest dynamics without occasional large wind throw events, *E. cordifolia* was now maintained indefinitely in the forest, where few large *E. cordifolia* trees accounted for a large proportion of the stand's basal area. Fluctuations of stem numbers and basal area were stronger than in the simulations without disturbances because of the effects of wind throw events.

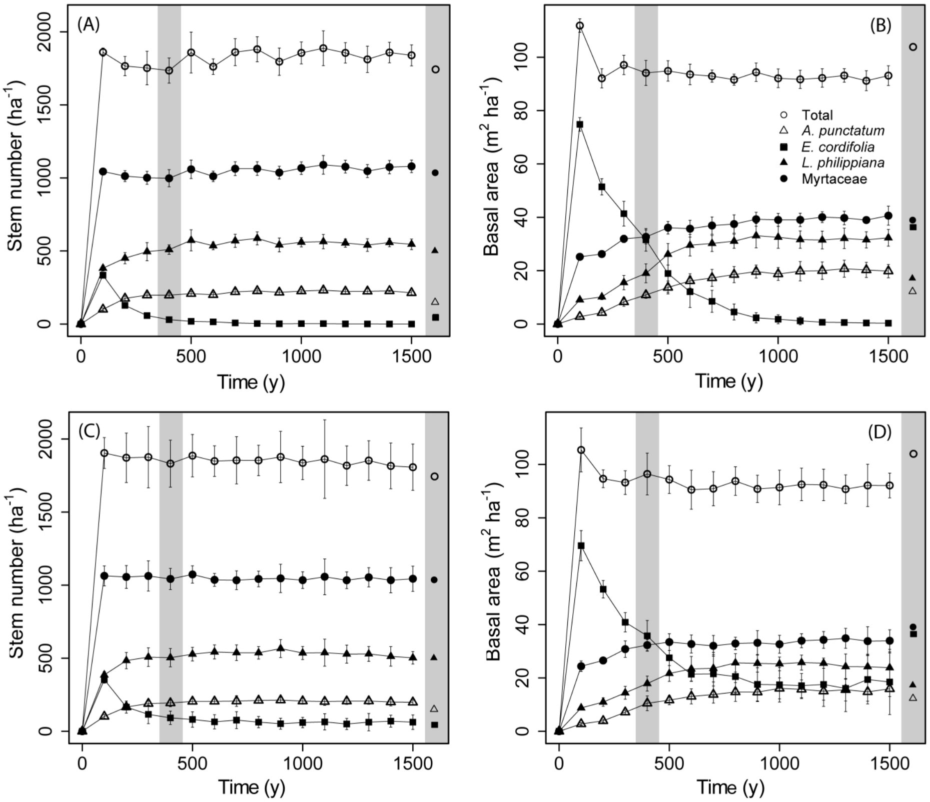


Figure 7.5 Simulation of forest regeneration after large-scale disturbance (e.g. clear-cut) without (A, B) and with (C, D) occasional wind throw events. Mean and standard deviation of stem numbers (A, C) and basal area (B, D) for all individuals ≥ 5 cm dbh and 10 simulations. Simulations were run for 1 ha and 1500 years. Inventory data from the study site (estimated age: 400 years) are shown in the grey bars on the right side of each chart.

7.3.2 Logging scenarios

Total harvest – We simulated wood extraction for three logging strategies (selective logging with and without remaining large old trees, and logging in bands). For selective logging scenarios, harvest aim converted to an annual basis varied from 1 to 10 m^3/ha. Total harvest over 400 years of simulated forest management (H) did not increase linearly with harvest aim, because the harvest aim could not always be reached.

For the selective logging scenarios with remaining large trees (> 1 m), H increased linearly up to a harvest aim of 5 m^3/ha (Fig. 7.6A). Then the increase of H began to slow down and saturated at about 2500 m^3/ha because with increasing logging intensity more logging operations had to be omitted due to the lack of harvestable trees. For a logging cycle of 50 years, the highest levels of wood extraction (450 and 500 m^3/ha) could never be achieved and no logging took place.

In the selective logging scenarios where large trees (> 1 m) were removed prior to management, *H* increased linearly up to a harvest aim of 6 m³/ha and then saturated at 3000 m³/ha (Fig. 7.6B). Again, for a logging cycle of 50 years, the highest levels of wood extraction (450 and 500 m³/ha) could never be achieved

Logging in bands achieved highest *H* that ranged from 2400 m³/ha (6 m³/ha per year) for a logging cycle of 150 years to 5360 m³/ha (13.4 m³/ha per year) for a logging cycle of 60 years (Fig. 7.6C).

Note: To make the logging scenarios comparable in regard to their ecological implications, *H* was transformed into mean annual harvest and ecological impacts were displayed relative to it.

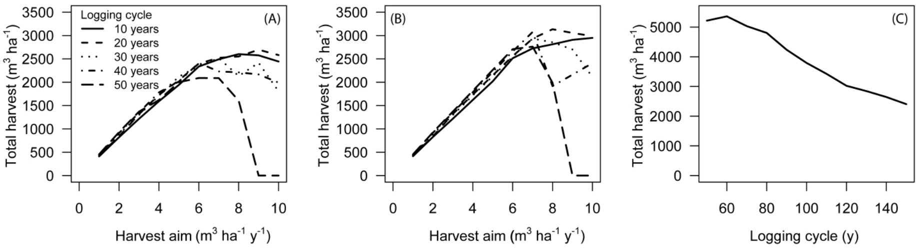


Figure 7.6 Total harvest over a logging period of 400 years for three logging strategies. Selective logging of trees 50 – 100 cm dbh with larger trees remaining standing (A) and with larger trees logged prior to the logging period (B). Logging cycle varied from 10 to 50 years, harvest aim (i.e. amount of extracted wood aimed at by the logging scenario) varied from 10 to 500 m³/ha, depending on the logging cycle. Thus, converted to an annual basis, harvest aim ranged between 1 and 10 m³/ha · y. Logging in bands (C) where each band is clear-cut every 50 – 150 years.

Forest composition – Impacts of logging scenarios on forest composition were measured for the four species by importance values (*IV*) which are based on relative stem numbers and basal area. Logging scenarios mainly had an effect on *IV*s of *E. cordifolia* and *L. philippiana* (Fig. 7.7). *IV*s of *E. cordifolia* were more than twice as high in the logging in bands scenarios than in the selective logging scenarios. This increase occurred at the expense of *L. philippiana* for which *IV*s in the logging in bands scenarios halved compared to selective logging. The inverse pattern was observed within the selective logging scenarios for increasing levels of wood extraction. While *E. cordifolia*'s *IV*s decreased, *IV*s of *L. philippiana* increased. *IV*s of *A. punctatum* remained relatively stable under the different logging scenarios. The myrtaceous species showed the same trends as *L. philippiana*, but to a lesser extend.

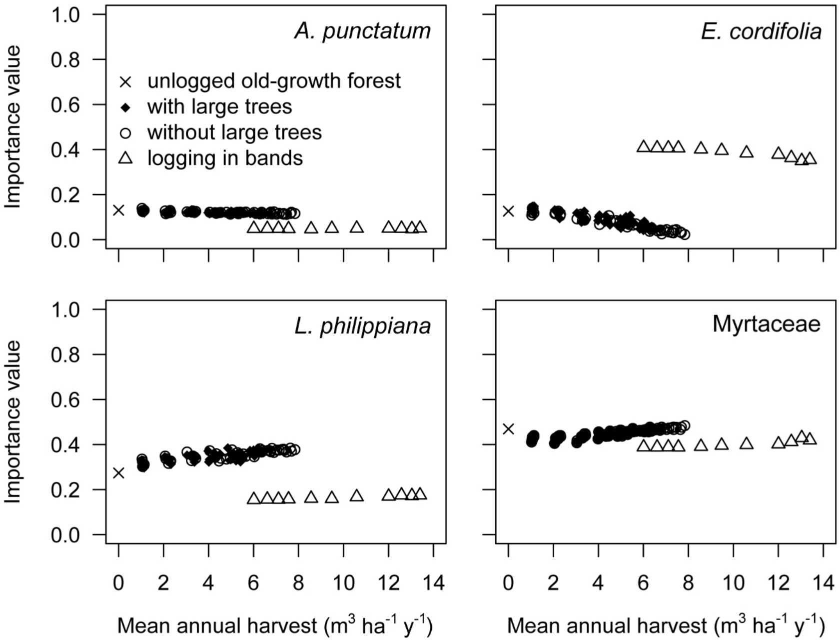


Figure 7.7 Impact of logging intensity on importance values ((relative abundance + relative basal area)/2) for four species and three logging strategies. Values of simulated unlogged old-growth forest are displayed for comparison (×).

Forest structure – To study the impact of logging scenarios on forest structure, we divided the trees into three diameter classes (5 – 50, 50 – 100, 100 – 200 cm dbh). The number of small trees (5 – 50 cm dbh) increased for increasing levels of wood extraction (Fig. 7.8A). The number of large trees (50 – 100 cm dbh) remained stable for low levels of wood extraction (up to 5 m^3/ha per year), but sharply decreased for higher levels of wood extraction (Fig. 7.8B). For logging in bands scenarios the decrease occurred at higher levels of wood extraction (8 – 14 m^3/ha per year). The number of old trees (> 1 m dbh) decreased linearly up to a mean annual harvest of 8 m^3/ha (Fig. 7.8C). Beyond that threshold, no old trees remained in the forests in the long term because large trees were harvested before they attained a dbh of 1 m.

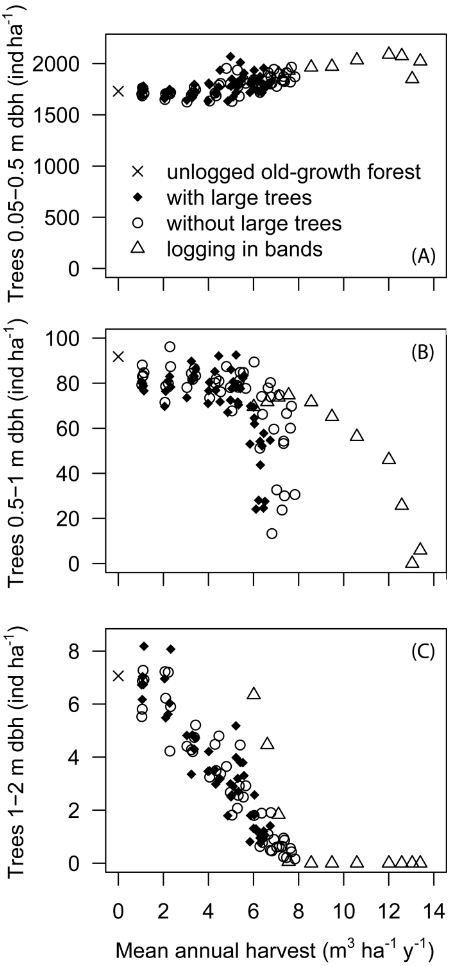


Figure 7.8

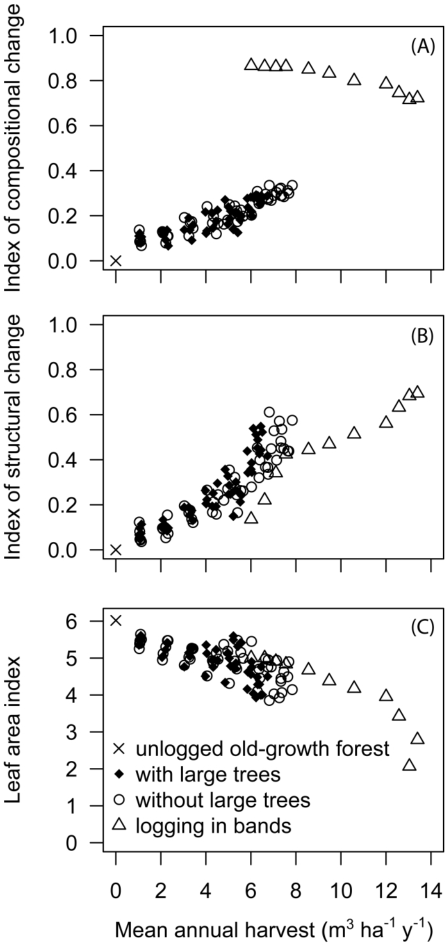
Impact of logging intensity on forest structure (i.e. stem numbers in three diameter classes) for four species and three logging strategies. Values of simulated unlogged old-growth forest are displayed for comparison (×).

Ecological indices – The index of compositional change (*ICC*) combines the differences in *IV*s of the different species compared to a simulated forest without logging. *ICC* increased with increasing levels of wood extraction for selective logging scenarios (Fig. 7.9A). *ICC* was very high (≈ 0.8) for all logging in bands scenarios and remained relatively stable regardless of the level of wood extraction.

The change in stem numbers in the three diameter classes compared to an unlogged forest is summarised in the index of structural change (*ISC*). *ISC* increased almost linearly with increasing levels of wood extraction (Fig. 7.9B). Only the selective logging scenarios with highest logging intensities altered the forest structure more than proportionally. Logging in bands with comparably low mean annual harvest (i.e. long logging cycles) had a lower impact on forest structure than selective logging scenarios with similar mean annual harvests.

Leaf area index (*LAI*) decreased from about 6 for low levels of wood extraction to about 4 for intermediate levels of wood extraction (Fig. 7.9C). *LAI* further decreased to about 2 – 3 for highest levels of wood extraction in logging in bands scenarios.

Figure 7.9



Impact of logging intensity on (A) the index of compositional change (*ICC*), (B) the index of structural change (*ISC*), and (C) leaf area index for three logging strategies. Values of simulated forest without logging are displayed for comparison (×). See section 7.2.6 *Assessment of logging scenarios* for a description of indices.

Ecological integrity vs. harvest – With increasing harvesting intensity, similarity to undisturbed old-growth forest (*EI*) decreased almost linearly for selective logging scenarios (Fig. 7.10). Hence, every surplus in the amount of harvested wood was accompanied by an increase of ecological impact. *EI* of band logging scenarios remained relatively stable at a low level. Compared to bare soil and a pure *Eucalyptus* plantation, however, selective logging scenarios are still relatively benign in terms of ecological impact. This is mainly due to the conservation of the native species composition and a higher LAI.

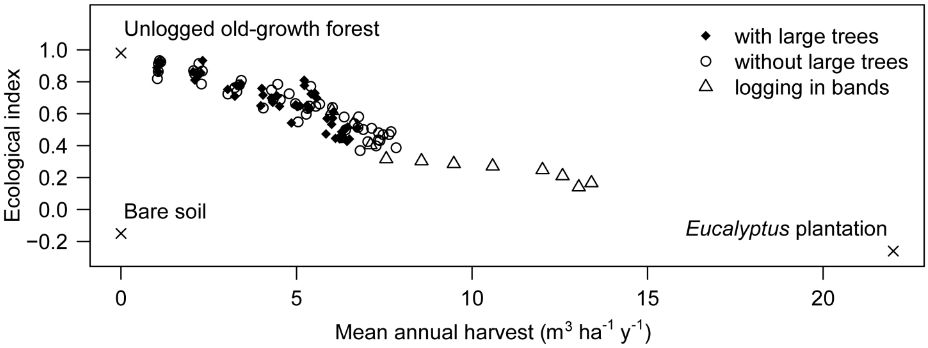


Figure 7.10

Impact of logging intensity on the ecological index (*EI*) for three logging strategies. Values of simulated unlogged old-growth forest, bare ground, and a simulated monospecific *Eucalyptus* plantation are displayed for comparison.

Discussion

7.4

FORMIND has proven to be a valuable tool for studying long-term forest dynamics of species-rich tropical rain forests (e.g. Kammesheidt et al. 2001, 2002, Köhler et al. 2001, 2003, Huth et al. 2004, 2005). Here, we parameterised FORMIND for the first time for a temperate rain forest in south-central Chile to identify ecological impacts of potential harvesting strategies. The individual-based approach allowed us to compare model results with field observations on different hierarchical levels such as individuals, populations, and the entire tree community (Grimm et al. 2005). Moreover, it enabled the detailed incorporation of different harvesting strategies. Logging in bands achieved highest harvests, but at the same time caused strong alterations of forest structure, composition, and LAI. Selective logging provided lower harvests, but better conserved old-growth forest characteristics.

Forest dynamics

7.4.1

The forest model is in agreement with empirical observations that natural medium- to large-size canopy openings (e.g. multiple tree falls during storm events) are necessary to maintain the characteristic species composition of Valdivian temperate rain forests. The model confirms that *Eucryphia cordifolia*, a relatively light-demanding tree species, depends on large canopy openings for regeneration (Veblen et al. 1981, Donoso et al. 1984, 1985, Veblen 1985). Without such disturbances that also affect much of the advance regeneration of shade-tolerant species, the abundance of *E. cordifolia* declines. Only few large trees remain in the forest because of *E. cordifolia*'s long lifespan that has been estimated to be at least 400 years (Lusk and del Pozo 2002, Gutiérrez et al. unpubl. manuscript). The dominance of shade-tolerant species increases over time and after 1000 years without medium to large-size disturbances they may dominate the forest almost completely (e.g. Donoso et al. 1984, 1985, Veblen 1985). Forest dynamics of temperate evergreen rain forest in the Coastal range of southern Chile is greatly related to the long lifespans of the tree species compared to other temperate forests where large-scale disturbances are more frequent (e.g. Veblen et al. 1980, Lusk and del Pozo 2002). When medium-size disturbances are implemented, *E. cordifolia* is maintained in the forest, although with lower basal area values than reported by inventory data from the study site.

Inventory data provide relevant information on forest dynamics, structure and composition. However, at the scale of inventory data (0.4 ha), the forests of the study region are heterogeneous in terms of forest structure and composition. The available inventory data correspond to old-growth forest with large, old *E. cordifolia* trees in the canopy, but lacking *E. cordifolia* regeneration, and represent this spatial heterogeneity only partly. This may explain why the model was unable to reproduce the high basal area in general, and of *E. cordifolia* in particular, recorded by field inventories. Therefore, field data from larger areas, including forest gaps, would provide a better sample for model evaluation.

7.4.2 Ecological impacts of harvesting strategies

Selective logging and logging in bands are two largely contrasting harvesting strategies. Logging in bands achieved highest harvests of up to 13 m³/ha·y. Maximum sustainable harvest of selective logging only reached 7.5 m³/ha·y when large trees were removed before forest management started, and 6 m³/ha·y when large trees remained in the forest. On the other hand, logging in bands altered forest composition and structure much stronger than selective logging. The stands created by this type of management were dominated by *E. cordifolia* with an understorey of shade-tolerant species. Selective logging favoured *L. philippiana* and the myrtaceous species, which benefited from the small gaps created by the logging operations.

Under the most yielding band logging scenarios no large, old trees (>1 m dbh) remained. The forest was converted into a secondary forest with a more homogeneous structure and a larger number of small trees. For selective logging scenarios, the number of large, old trees also decreased with increasing harvest intensity, but the structural complexity of the forest was better maintained. Mature and senescent trees play important roles as habitat for many animal and plant species, such as woodpeckers or vascular and non-vascular epiphytes (e.g. Angelstam and Mikusiński 1994, Franklin and Armesto 1996, Galloway 1999, Arroyo et al. 1999a, Lindenmayer and Franklin 2002, Díaz et al. 2005). Therefore, we recommend the retention of some large, old, and dead trees to conserve components of biodiversity that depend on them as well as to increase structural complexity of logged forests (Armesto et al. 1999c).

Due to the low level of atmospheric nutrient input and the high rainfall, it is essential that sustainable forest management in this region ensures a relatively continuous canopy cover to prevent soil erosion and maintain biological processes such as nutrient retention and recycling (Hedin et al. 1995, Galloway et al. 1996, Pérez 1999). In the model, LAI of single trees is 4 (cf. Saldaña and Lusk 2003). Therefore, logging strategies should maintain LAIs of at least 3 for the entire forest stand to ensure a sufficient canopy cover. The two band logging scenarios that provide highest harvests do not satisfy this requirement.

Recent studies suggest that silvicultural treatments should mimic natural disturbance regimes to minimise negative effects on biodiversity and ecological processes (e.g. Perry 1994, Armesto et al. 1996, Smith et al. 1996, Lindenmayer and Franklin 2002). In the study area, the natural disturbance regime comprises frequent single or multiple tree falls that create canopy gaps usually smaller than 400 m² (Armesto and Fuentes 1988, Armesto et al. 1999b), and rarer wind throw events that affect larger areas. The simulated low-intensity logging mimics natural gap creation by single tree falls and logging in bands can be regarded as a form of simulating medium size disturbances. Smaller canopy gaps favour advanced regeneration of shade tolerant species already present in the understorey, whereas regeneration of *E. cordifolia* is enhanced by larger gaps. To maintain spatial heterogeneity, the creation of gaps of different sizes could be incorporated into future forest management planning. At the same time, this would allow for aggregated retention of original forest structures (Armesto et al. 1999c, Lindenmayer and Franklin 2002).

Annual volume increment of the most productive simulated selective harvesting scenarios (up to 7.5 $m^3/ha \cdot y$) and logging in bands scenarios (up to 13 $m^3/ha \cdot y$) lies in the range of estimates of annual volume increments for young managed stands of *Nothofagus alpina* (up to 10 $m^3/ha \cdot y$), *N. dombeyi* and *N. alpina* (7–12 $m^3/ha \cdot y$), or *Drimys winteri* (8–15 $m^3/ha \cdot y$) (Grosse and Quiroz 1999, Navarro et al. 1999). Thus, our estimates indicate that the native old-growth forests can be a valuable source for constant and sustainable timber harvest.

Limitations of model application 7.4.3

A potential shortcoming of the model is the omission of the understorey bamboo species *Chusquea quila* which is known to be an aggressive coloniser of canopy gaps. *Chusquea* has been reported to inhibit tree regeneration (e.g. Donoso 1989b, González et al. 2002, Donoso and Nyland 2005). Likewise, the pioneer tree species *Drimys winteri* has been ignored for the time being. Both species are absent or rare at the study site, but can be expected to respond positively to human intervention and to have a considerable impact on forest dynamics (e.g. Veblen 1982, Donoso 1989a). Consequently, further simulation studies on forest management should incorporate them.

An important assumption underlying our simulations of forest dynamics and management is that nutrient limitation is of minor importance. For the studied ecosystem, the nutritional balance strongly depends on the maintenance of intact biological processes of nutrient retention and recycling and therefore massive biomass extraction should be avoided (Arroyo et al. 1999b, Pérez 1999). Thus, model results have to be analysed keeping this restriction in mind.

All simulations in this study assume that regeneration rates of the different species are spatially homogeneous. For forest dynamics on a larger spatial scale this simplification may be of minor importance, but for studies of spatial heterogeneity on a small scale, regeneration should be coupled to the forest composition in the neighbourhood and different dispersal abilities should be incorporated. The necessary routines are available in the model, but were here switched off to reduce the number of model parameters and parameterisation effort.

7.4.4 Outlook

The applied approach is a first step towards an analysis of management strategies for VTRF in southern Chile that serve multiple purposes such as wood production and maintenance of complex forest structure to ensure the protection of ecosystem services (e.g. soil conservation, water quality, habitat for biodiversity, cultural and recreation values). However, assessment of economic aspects is still rudimentary, and needs enhancement if model results are to be used by decision makers and stake holders that depend on the forest as a source of income. To make results more meaningful to forest owners, economic concepts, such as discounting and price development, have to be taken into account. Simulation of management scenarios for secondary forests should be given priority as these are managed more often than old-growth forests and because of their high potential for timber and fuelwood production (e.g. Donoso et al. 1999). For a better model evaluation it would be very helpful if inventory data from young secondary forests became available.

The model provides an opportunity to explore the implications of potential management options and to raise awareness and understanding of the underlying ecological processes of forest dynamics. Simulation exercises can support forestry education in Chile, where the conventional forestry is largely based on the management of exotic tree plantations, with respect to management of native forests (Lara et al. 2003).

7.5 Conclusions

This study shows that species-rich Valdivian temperate rain forest in south-central Chile has a high potential for provision of timber and fuelwood. Simulated harvesting scenarios represent a wide range of possible management strategies, each of which achieves a different balance between wood production and conservation of old-growth forest characteristics. The more wood is harvested the stronger is the alteration of forest structure and composition. Logging in bands promotes the regeneration of the relatively light-demanding and fast-growing *Eucryphia cordifolia*, whereas selective logging favours shade-tolerant species such as *Laureliopsis philippiana*. Forest structure was simplified in all logging scenarios, and large, old trees decreased sharply in abundance. Management strategies that rely on native species and keep an uneven-aged forest structure ensure the maintenance of native species diversity, protect ecosystems from exotic species invasions, and promote the conservation of essential mutualistic interactions. Thus, they can contribute to a diversification of land use against the background of an increasing replacement of native old-growth forests by plantations of exotic tree species, agriculture, or other land uses.

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Appendix Sensitivity analysis

7.7

Methods

We used the software package SimLab2.2 (Simulation environment for uncertainty and sensitivity analysis) to explore the impact of model parameters on model results. We applied the extended FAST method (Fourier Amplitude Sensitivity Test) to compute first order sensitivity indices (Saltelli et al. 2000). The FAST method is a variance-based method that avoids making the assumption that model parameters and output are nearly linearly related on which regression-based methods rely. If Y is the model output and X_i the parameter of interest, then the first order sensitivity index

$$S_i = \frac{V(E(Y|X_i))}{V(Y)}$$

indicates the amount of variance that would be removed from the total output variance if the parameter's true value was known, and hence the relative importance of a given model parameter for a given model prediction (Tarantola et al. unpubl. manuscript). If X_i has a strong impact on Y, then $E(Y|X_i)$ varies strongly with X_i, and hence $V(E(Y|X_i))$ is high. If X_i has a low impact on Y, then $E(Y|X_i)$ will be relatively constant and $V(E(Y|X_i))$ is low. For an additive model, the sum of first order sensitivity indices is 1. For non-additive models the sum is < 1, and the difference

$$1 - \sum_i S_i$$

indicates the degree of non-additivity of the model, i.e. the importance of interactions between model parameters.

We simultaneously varied all model parameters in a range of +/– 20 % of their standard value. Simulations were run for 119 770 parameter combinations for 1 ha and 1000 years. The initial situation was derived from inventory data of old-growth VTRF in Guabún, northern Chiloé Island, Chile. Selected model predictions are aggregated forest characteristics such as stem volume, biomass, basal area, stem number, and leaf area index of the entire forest stand, as well as basal area, stem number, maximum diameter increment and maximum age for each species. Model predictions were evaluated at ten points in time (every 50 years from simulation time 550 to 1000 to allow the model to reach a steady state) and averaged.

Results

Aggregated forest characteristics – Aggregated forest characteristics, namely total stem volume (*SV total*), biomass (*BM total*), basal area (*BA total*), stem number (*N total*), and leaf area index (*LAI*) are most strongly affected by the parameter of the linear relationship between stem diameter and crown diameter (*cd*), the light extinction coefficient (k), the proportion of stem wood biomass to total biomass (*sw*), the LAI of a single tree (L_{max}) (Fig. 7.A). Average irradiance above the canopy (I_0) is a parameter of intermediate importance. Total stem number is additionally influenced by the parameters of increased mortality of small trees (m_{max}, D_{mort}), and total basal area by several characteristics of the myrtaceous species (form factor f, maximum photosynthetic capacity p_{max}, slope of light-response-curve α, wood density ρ, maintenance respiration parameter r_0).

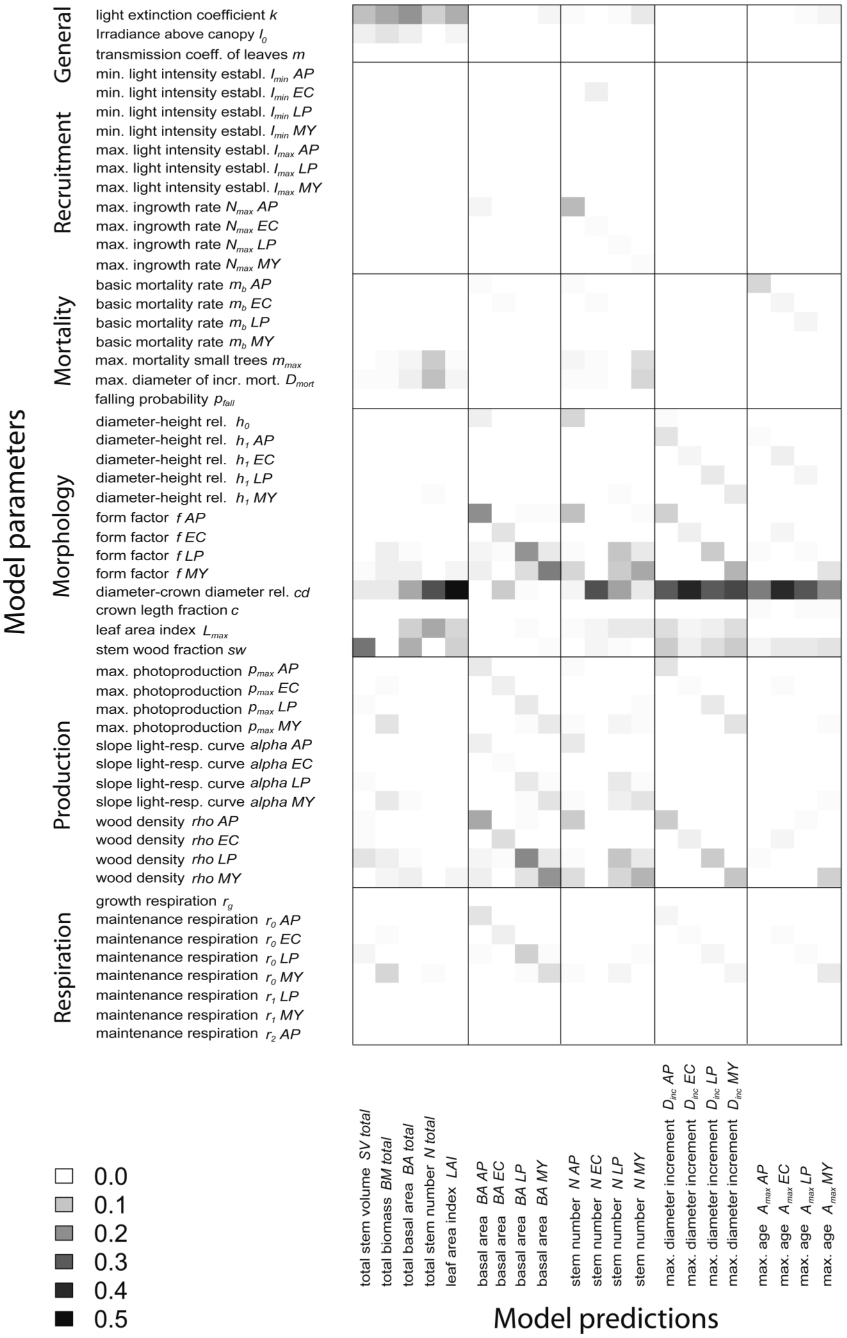
Basal area – Basal area of the different species (*BA AP*, *BA EC*, *BA LP*, *BA MY*) is most strongly affected by production parameters (maximum photosynthetic capacity p_{max}, slope of light-response-curve α, wood density ρ). Additionally, the form factor (f), and to a lower extent, the respiration parameter (r_0), have an effect.

Stem numbers – Stem numbers of the different species (*N AP*, *N EC*, *N LP*, *N MY*) are most strongly affected by production and morphological parameters (slope of light-response-curve α, wood density ρ, form factor f, the parameter of the linear relationship between stem diameter and crown diameter *cd*). The number of individuals of myrtaceous species (*N MY*) is also significantly influenced by the size-dependent component of mortality (m_{max}, D_{mort}). The only recruitment rate that has an impact on stem numbers is the one of *A. punctatum* (N_{max} *AP*). Stem numbers of *E. cordifolia* depend on minimum light intensity required for its establishment (I_{min} *EC*).

Maximum diameter increment – For all species, maximum diameter increment is most strongly affected by the parameter of the linear relationship between stem diameter and crown diameter (*cd*). A parameter of the diameter-height relation (h_1), form factor (f), LAI per tree (L_{max}), stem wood fraction (*sw*), maximum rate of photosynthesis (p_{max}), wood density (ρ), and a parameter describing maintenance respiration (r_0) have intermediate effects on maximum diameter increment.

Maximum age – Again, the parameter with the strongest influence is the parameter of the linear relationship between stem diameter and crown diameter (*cd*). Mortality rates (m_b) and stem wood fraction (*sw*) are of minor importance.

Figure 7.A First order sensitivity indices for model parameters on selected model predictions regarding overall forest characteristics (*SV*, *BM*, *BA*, *N*, *LAI*), species composition (*BA*, *N* for the different species), maximum diameter increment (D_{inc}), and maximum age (A_{max}). Indices were computed with the extended FAST method (Saltelli et al. 2000). *AP* = *A. punctatum*, *EC* = *E. cordifolia*, *LP* = *L. philippiana*, *MY* = *Myrtaceae*. A table with standard values of model parameters is given in Appendix A of the thesis.


Model parameters
General
Recruitment
Mortality
Morphology
Production
Respiration
light extinction coefficient k
Irradiance above canopy I_0
transmission coeff. of leaves m
min. light intensity establ. I_{min} AP
min. light intensity establ. I_{min} EC
min. light intensity establ. I_{min} LP
min. light intensity establ. I_{min} MY
max. light intensity establ. I_{max} AP
max. light intensity establ. I_{max} LP
max. light intensity establ. I_{max} MY
max. ingrowth rate N_{max} AP
max. ingrowth rate N_{max} EC
max. ingrowth rate N_{max} LP
max. ingrowth rate N_{max} MY
basic mortality rate m_b AP
basic mortality rate m_b EC
basic mortality rate m_b LP
basic mortality rate m_b MY
max. mortality small trees m_{max}
max. diameter of incr. mort. D_{mort}
falling probability p_{fall}
diameter-height rel. h_0
diameter-height rel. h_1 AP
diameter-height rel. h_1 EC
diameter-height rel. h_1 LP
diameter-height rel. h_1 MY
form factor f AP
form factor f EC
form factor f LP
form factor f MY
diameter-crown diameter rel. cd
crown legth fraction c
leaf area index L_{max}
stem wood fraction sw
max. photoproduction p_{max} AP
max. photoproduction p_{max} EC
max. photoproduction p_{max} LP
max. photoproduction p_{max} MY
slope light-resp. curve $alpha$ AP
slope light-resp. curve $alpha$ EC
slope light-resp. curve $alpha$ LP
slope light-resp. curve $alpha$ MY
wood density rho AP
wood density rho EC
wood density rho LP
wood density rho MY
growth respiration r_g
maintenance respiration r_0 AP
maintenance respiration r_0 EC
maintenance respiration r_0 LP
maintenance respiration r_0 MY
maintenance respiration r_1 LP
maintenance respiration r_1 MY
maintenance respiration r_2 AP
total stem volume SV total
total biomass BM total
total basal area BA total
total stem number N total
leaf area index LAI
basal area BA AP
basal area BA EC
basal area BA LP
basal area BA MY
stem number N AP
stem number N EC
stem number N LP
stem number N MY
max. diameter increment D_{inc} AP
max. diameter increment D_{inc} EC
max. diameter increment D_{inc} LP
max. diameter increment D_{inc} MY
max. age A_{max} AP
max. age A_{max} EC
max. age A_{max} LP
max. age A_{max} MY
Model predictions
0.0
0.1
0.2
0.3
0.4
0.5

Discussion

Model predictions were most strongly affected by model parameters that describe the photosynthesis and morphology of individual trees. The maximum diameter increment of all species was most strongly affected by the parameter of the linear relationship between stem diameter and crown diameter (*cd*). LAI per tree (L_{max}) and *cd* determine how much leaf area of a tree is available for photosynthetic production. Parameters related to biomass allocation (e.g. wood density (ρ) and form factor (f)) play an important role because they define how biomass increment is translated to diameter increment.

The parameters *cd*, L_{max}, light extinction coefficient (k), and the ratio of wood biomass to total biomass (*sw*) have the largest effects on aggregated forest characteristics such as total stem volume, biomass, basal area, stem numbers, and LAI. The parameters *cd* and L_{max} determine the stand's leaf area and k controls how incoming light is absorbed through the canopy. These parameters influence the most important process of the forest model – competition for light due to shading – and determine forest productivity and biomass. Parameter *sw* has an impact on stem volume and basal area, because it determines the proportion of biomass allocated to the stem.

The same parameters that were important for maximum diameter increment (*cd*, h_1, f, L_{max}, *sw*, p_{max}, ρ, r_0), were also important for the species composition of the forest in terms of basal area and stem numbers for the different species. This may be an indication that tree growth is a very important process and that growth characteristics of the different species largely determine species composition of the forest (cf. Lusk and Matus 2000). Recruitment and most mortality parameters only had minor impacts on model predictions.

A previous sensitivity analysis of FORMIND with the parameterisation for a tropical lowland rain forest in Venezuela obtained very different results (Kammesheidt et al. 2001). In their study, model parameters related to recruitment and mortality most strongly affected species composition. This difference may be due to different types of sensitivity analysis applied. Kammesheidt et al. (2001) varied only one model parameter at the time. For high dimensional non-linear models, however, global sensitivity analyses are more appropriate (Saltelli et al. 2000).

First order sensitivity indices reveal which model parameters provide opportunities to significantly reduce uncertainty of simulation results. According to our results, more detailed information on morphological parameters, as well as on physiological processes such as photosynthesis and respiration are needed for Chilean trees, in order to improve the data basis for process-based forest models.

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General discussion 8

Synthesis of findings from model applications 8.1

In the previous four chapters, the forest growth model FORMIND has been applied to study natural forest succession as well as productivity and ecological impacts of different management scenarios of native species-rich tropical montane cloud forest in central Veracruz, Mexico, and Valdivian temperate rain forest in northern Chiloé Island, Chile. The first part of the general discussion is aimed at summarising and comparing the results for the two study regions as well as drawing general conclusions for a sustainable use of species-rich moist forests.

Forest dynamics 8.1.1

The most conspicuous difference between tropical montane cloud forest (TMCF) in central Veracruz, Mexico, and Valdivian temperate rain forest in southern Chile (VTRF) is their tree species richness. In TMCF more than 100 tree species have been counted (G. Williams-Linera, pers. comm.), whereas in VTRF about 15 tree species occur (Donoso 1993). The forests also differ largely in their structure and dynamics due to differences in life-history traits of the tree species and the disturbance regime in the study regions.

In TMCF, the trees grow fast (up to 2 cm/y; Williams-Linera 1996). Tree lifespans seem to be short and large old trees rarely exceed a maximum diameter of 1 m. The model estimates an annual turnover rate of 5% (trees ≥ 5 cm dbh) which corresponds to short-term observations from the study site (Williams-Linera 2002). In VTRF, the trees grow more slowly (up to 1 cm/y; A. Gutiérrez, unpubl. data). They reach maximum diameters of up to 2 m (especially *Eucryphia cordifolia*), and have longer lifespans (e.g. Lusk and del Pozo 2002). The model suggests that annual turnover rates are as low as 2% (trees ≥ 5 cm dbh).

According to simulation results, TMCF regenerates rapidly after disturbance, and field data confirm this (Muñiz-Castro et al. in press). After a few decades, aggregated forest characteristics such as density, basal area, and leaf area index (LAI) have recovered. The successional dynamics of TMCF corresponds to the typical temporal pattern: an initial stage dominated by pioneer species is followed by an intermediate stage where species with intermediate shade tolerance gain the highest basal area values, and finally a climax stage where shade-tolerant species attain their maximum share. Forest structure and species dominance in terms of basal area of different plant functional types (PFTs) reach a steady state and old-growth conditions within 300 years after a large-scale disturbance.

Like in TMCF, aggregated characteristics of VTRF recover rapidly but the temporal pattern of the succession is different and the dynamics is slower. Following a large-scale disturbance, the light-demanding *E. cordifolia* dominates in terms of basal area for about 400 years. Then *E. cordifolia* is slowly replaced by shade-tolerant species and tends to disappear from the forest after about 800 years if no medium to large-sized disturbances occur. The proportion of basal area of the different species reaches a steady state after approximately 1000 years.

With a basal area of about 45 m^2/ha and an above-ground biomass of 480 Mg/ha, TMCF in central Veracruz stores more biomass than Amazonian tropical lowland rain forests where basal area values of 25 – 30 m^2/ha were measured and estimated biomass ranged between 220 and 340 Mg/ha (Baker et al. 2004). With a density of about 1800 ind/ha (≥ 5 cm dbh) and a basal area of nearly 100 m^2/ha, VTRF belongs to the densest forests with highest stem volume (up to 1000 m^3/ha) (Armesto et al. 1999a) and biomass (800 Mg/ha) of the world. Volume increments of TMCF and VTRF are similar due to the rapid growth of TMCF and the large amount of biomass of VTRF.

The differences in forest dynamics and structure are possibly due to differences in the disturbance regime in both regions. In central Veracruz (TMCF), the prevalent disturbance regime is gap creation on a small spatial scale, because most of the dying trees fall over and only a small portion remains standing (Williams-Linera 2002). Natural large-scale disturbances such as hurricanes, land slides, fire, or floods are rare and negligible for forest dynamics (G. Williams-Linera, pers. comm.). In northern Chiloé Island (VTRF), the disturbance regime seems to be composed of single and multiple-tree falls, which apparently occur with lower frequency than in TMCF, and infrequent wind throw events which open much larger gaps of up to several hectares (A. Lara, pers. comm.). Tree species that dominate early successional phases of VTRF such as *E. cordifolia*, *Drimys winteri*, or *Embothrium coccineum* are not able to successfully establish in small canopy gaps but require large canopy openings, whereas in TMCF, pioneer species and species with intermediate shade tolerance are able to establish in single tree fall gaps.

In old-growth VTRF, LAI is very high and light levels at the forest floor are low (Saldaña and Lusk 2003). Thus, *E. cordifolia* can only survive in the forest due to its long lifespan*, that allows it to persist in the forest until a new large disturbance occurs, and its emergent stature that assures a wide distribution of the wind dispersed seeds. Hence, *E. cordifolia* is an example of the rare long-lived pioneer species (e.g. Loehle 1988, Lusk 1999). On the contrary, the majority of tree species of VTRF is adapted to low light levels and can establish and persist underneath a closed canopy (cf. Figueroa and Lusk 2001, Lusk and del Pozo 2002).

The occurrence of large-scale disturbances together with long tree lifespans also causes a high spatial heterogeneity of VTRF. Gaps of different size, young dense patches, old-growth forest with emerging *E. cordifolia*, and forest patches where *E. cordifolia* is lacking and shade-tolerant species dominate occur side by side on a large spatial scale. This spatial heterogeneity is difficult to cover with conventional inventory data in small sample plots. Thus, in terms of forest structure, VTRF is more heterogeneous than TMCF and can be regarded to be "in equilibrium" only on very large temporal and spatial scales.

* Lusk and del Pozo (2002) suggest that the published maximum age of 400 years for *E. cordifolia* greatly underestimates potential longevity.

Forest productivity 8.1.2

On a global scale, and in the context of increasingly globalised wood fibre production, sustainable management of native forests in Mexico and Chile is not likely to be competitive from the economic point of view (Franklin 2003). Quantitatively, annual wood volume increments of up to 12 m^3/ha in Mexican TMCF and up to 13 m^3/ha in Chilean VTRF fall well short of growth rates of plantations of *Eucalyptus* spp. or *Pinus radiata* which reach mean annual volume increments of 40 and 30 m^3/ha, respectively (Ugalde and Pérez 2001). In Mexico, the current mean annual yield from the management of native forests is as low as 1.2 m^3/ha, and in a sustainable development scenario this value is envisioned to rise to 1.8 m^3/ha until the year 2025 (Torres-Rojo 2004). The simulated maximum sustainable harvest suggests that Mexican TMCF has a much higher potential for wood production, although simulated wood extraction rates refer to gross stem volume values and not to net commercial volume. Simulated annual volume increments are also much higher than those predicted for various tropical lowland forests ranging between 1 and 4 m^3/ha (Huth and Ditzer 2001, Kammesheidt et al. 2002, van Gardingen et al. 2003). However, Silva et al. (1995) measured an annual volume increment of 6 m^3/ha directly after the logging of rain forest in the Brazilian Amazon.

Annual wood volume increment is highest for young forests that are dominated by fast-growing tree species with an intermediate shade tolerance, i.e. when the forests are artificially kept in an intermediate successional stage. In both study regions, the management of secondary forests is promising and could serve as an alternative to an exploitation of virtually undisturbed old-growth forests (e.g. Donoso et al. 1999). Selective logging of Chilean VTRF favoured shade-tolerant species, whereas *E. cordifolia* regeneration was promoted by clear-cutting in bands. Clear-cutting in bands creates larger gaps which are more suitable for the establishment of *E. cordifolia*. The same rationale applies to other shade-intolerant commercial tree species (e.g. mahogany (*Swietenia macrophylla*)), that do not sufficiently regenerate after selective logging to sustain desired yields (e.g. Fredericksen and Putz 2003, and references therein). Thus, successful management of native species-rich forests requires an adaptation of management practices to the ecological properties of the target species.

Compared with plantations of non-native species, sustainable management of the native forests can provide a continuous supply of timber and fuelwood and has ecological and economic advantages that might offset the lower growth rates under certain circumstances (Franklin 2003). Economic advantages include lower management costs for small owners or local communities, the proximity of wood production to local markets, and a higher timber quality. From the ecological perspective, the management of native forests improves the quality of the land use. The conservation of native biodiversity assures the maintenance of mutualistic interactions (Armesto et al. 1999a, Smith-Ramírez 2005), the regulation of hydrological cycles (e.g. Iroumé and Huber 2002), the storage of higher amounts of carbon (e.g. Chen et al. 2005), or the supply of non-timber forest products.

8.1.3 Ecological impacts of logging and implications for conservation

I applied the forest growth model FORMIND to assess ecological impacts of alternative harvesting strategies in two forest types, TMCF in Mexico and VTRF in Chile. Ecological impacts on the forest were measured for three forest properties: species composition, forest structure, and LAI. The logged forest was compared to an undisturbed forest. Species composition was quantified by importance values that take into account relative density and basal area of the different species or plant functional types (PFT). Forest structure refers to stem numbers in three to five diameter classes. LAI can be regarded as an environmental indicator of erosion risk because bare ground is more prone to soil erosion than soil under a closed forest cover. Changes in species composition, forest structure, and LAI were aggregated into a single "ecological index" that measures the overall ecological impact of a given logging scenario.

A widely adopted definition of ecologically sustainable forest management is given by Lindenmayer and Recher (1998): "*Ecologically sustainable forest management perpetuates ecosystem integrity while continuing to provide wood and non-wood values; where ecosystem integrity means the maintenance of forest structure, species composition, and the rate of ecological processes and functions with[in] the bands of normal disturbance regimes*". However, every anthropogenic intervention in the form of wood extraction, even at a very low intensity, has an ecological impact on the forest. Thus, the above definition is, in a strict sense, impossible to fulfil. Tree felling is an additional disturbance which increases mortality, and this increased mortality has an effect on the forest structure and composition. The crucial point is rather: How severe are the ecological impacts? In all logging scenarios that were investigated in this thesis, the overall ecological impact in terms of the aggregated ecological index increased linearly with the amount of extracted wood. This linearity was also observed at the level of overall forest structure and composition, but not at the level of single PFTs or diameter classes.

In logging scenarios in Mexican TMCF, the species composition shifted to species or PFTs that were not targeted by logging. When only species with intermediate shade tolerance were harvested, the shade-tolerant canopy species benefited. An increase of the abundance of pioneer species could not be detected. This is confirmed by field observations in central Veracruz (G. Williams-Linera, pers. comm.) and is attributed to a decrease of average gap size due to the lower number of very large falling trees. In VTRF in Chile, different harvesting strategies had a differential effect on the species composition of the forest. Selective logging of single trees favoured shade-tolerant species such as *Laureliopsis philippiana*, whereas logging in bands promoted the regeneration of the light-demanding *E. cordifolia*.

The most notorious effect of wood extraction on the forest structure was the loss of large old trees from the forest. Every kind of management that does not explicitly retain a number of large old trees lead in the long term to the loss of those trees, whereas the number of small trees increased. Thus, the forest structure simplified, the forests became younger and more homogeneous. These changes in the forest structure can take between a few decades and more than one hundred years and can therefore hardly be observed directly. The LAI values of the simulated logged Mexican TMCF, on the one hand, differed only slightly from those of undisturbed forests. The corresponding simulation results suggest that managed forests can provide ecosystem services such as water capture from clouds and soil protection largely to the same extent as old-growth forests. For Chilean VTRF, on the other hand, the two logging scenarios with the best harvests (logging in bands every 50 or 60 years) did not maintain LAI values regarded high enough to ensure adequate soil protection in this region with its exceptionally high levels of rainfall.

Management decisions are based on a multitude of different criteria which are given different priority by different stakeholders. Simulation results serve to define a type of management that balances conservation and production objectives according to these preferences. Apart from adjusting harvesting method and intensity, variable retention systems (SVR) provide a flexible means of combining different management objectives (e.g. Lindenmayer and Franklin 2002). SVR allows to define a certain amount of forest structures (e.g. large living trees, dead trees, undisturbed forest floor, patches of understorey shrubs and herbs, or groups of juvenile trees in a forest gap) to be left untouched facilitating the recovery of biodiversity and ecosystem processes, as well as ensuring the maintenance of islands of original habitat and landscape connectivity (Armesto et al. 1999b). This way, the loss of large old trees can be partially compensated. Areas with different amounts of retained elements and of varying extension can be combined to assure a spatially diverse forest structure.

Evaluation of the process-based modelling approach 8.2

FORMIND was developed for the simulation of the dynamics of species-rich moist forests where competition for light is the main driver for forest dynamics. It includes key processes such as recruitment, growth, mortality, competition for light and space, gap creation through falling dead trees, and external disturbances. Thus, it can be applied to all moist forests where competition for water and nutrients is of minor importance. The main focus of the model is on the response of the forest to natural and anthropogenic disturbances at the stand level and on the temporal scale of decades to hundreds of years. To cope with the high species richness of tropical forests, tree species are grouped into plant functional types (PFTs) according to their maximum height and light demand. FORMIND differs from most other models of mixed-species forests in the calculation of single-tree growth as the carbon balance of single trees is calculated on the basis of photosynthesis and respiration. The individual-oriented approach allows for a model evaluation on different levels (e.g. trees, PFTs, entire tree community).

Model parameterisation 8.2.1

FORMIND has 50 – 70 parameters depending on the number of species or PFTs that are represented. Compared to more empirical forest models which often contain hundreds of parameters, this number is rather low (e.g. Bugmann 2001). The parameters used in FORMIND can be divided into environmental parameters (e.g. average light intensity above the forest, light extinction coefficient), allometric parameters (e.g. relations between stem diameter, height, crown diameter, crown depth, form factor), physiological parameters (e.g. maximum rate of photosynthesis, slope of light-response-curve, respiration parameters), and demographic parameters (recruitment and mortality rates).

The data basis for parameter estimation is usually very heterogeneous. Environmental parameters and allometric relations of tree geometry are relatively easy to obtain from field measurements. Measurements of physiological parameters, on the other hand, are mostly unavailable, especially measurements of respiration parameters. However, field data on diameter increment of single trees, either from growth measurements over several years or from dendrochronological analyses, are often available. Thus, physiological parameters can be adjusted in such a way that observed growth characteristics are reproduced. In this study, a computational approach was applied to fit respiration parameters. A genetic algorithm was used to find respiration parameters such that simulated maximum tree growth best matched field data. For demographic parameters, almost no field data were available for the two study regions. Thus, model parameters were manually adjusted through trial and error until old-growth forest characteristics derived from inventory data from the study sites were reproduced. A computational approach to parameter fitting was discarded because the number of parameters seemed to be too high compared to the low amount and quality of field data (i.e. patterns) to apply a rigorous pattern-oriented modelling approach (Grimm et al. 1996, Wiegand et al. 2003, Grimm et al. 2005). This impression was confirmed by unsatisfying results of computational parameter fitting attempts with FORMIND for Brazilian tropical rain forests (J. Groeneveld, pers. comm.). However, the hierarchical parameter estimation assured that the different processes (e.g. recruitment, growth, mortality) were represented as best as possible on the basis of current knowledge on the forests of the study sites.

8.2.2 Model evaluation

Apart from the methods to derive model parameters from field data that were described in the previous paragraph and that to some extent assure that single processes produce realistic outcomes, independent field data were used to validate overall model results. Simulated LAI and irradiance at forest floor of TMCF in central Veracruz lay in the range of literature values reported for other TMCF sites in Mesoamerica. Simulated diameter distributions and overall mortality rate corresponded to field data from the study site. Furthermore, the results of a chronosequence study that covered 0.5 – 80 year old secondary TMCF in central Veracruz could be used to validate model predictions regarding the regeneration of TMCF (Muñiz-Castro et al. in press). The qualitative development of simulated forest regeneration corresponded to the field data. However, the model slightly overestimated the velocity of forest recovery due to a higher recruitment rate during the first decade and a slightly overestimated tree growth. The model predictions reflect reality astonishingly well, especially when taking into account that the model was calibrated to reproduce old-growth forest characteristics. It was not explicitly adapted for the special case of regeneration outside a closed forest. Hence, mechanisms that are potentially important for forest regeneration outside closed forests such as limited seed dispersal or increased mortality due to desiccation were not necessary to describe the coarse regeneration pattern. However, maybe these processes are responsible for the overestimation of the velocity of forest recovery. Thus, simulation results for harvesting scenarios of TMCF in central Veracruz seem to be reliable, although sustainable harvesting rates could be slightly overestimated due to the overestimated recruitment rates and tree growth.

No independent field data for VTRF in northern Chiloé Island were found that made a validation of simulation results possible. As a consequence, simulation results regarding dynamics and sustainable use of VTRF have to be interpreted carefully. They should be regarded as possible scenarios derived from currently available information on the forest. Due to the high spatial heterogeneity and insufficient understanding of the dynamics of VTRF, it would be desirable to obtain inventory data from larger areas, from secondary forests of different ages, as well as information about mortality rates and the frequency and extent of large-scale disturbances.

A sensitivity analysis was performed to identify the impact of single model parameters on model outcomes. It was the most extensive sensitivity analysis carried out with a model from the FORMIND/FORMIX model family so far. Previous sensitivity analyses investigated the impact of model parameters on simulation results by varying only one parameter at the time. For high-dimensional non-linear models, however, global sensitivity analyses are more appropriate (Saltelli et al. 2000). The parameter for the linear relationship between stem diameter and crown diameter had the highest impact for model outcomes. This parameter had the most significant impact on single tree growth as well as on overall forest characteristics such as LAI, density, and basal area. Thus, I conclude that growth characteristics of the different species or PFTs are of prominent importance for the species composition of the forests. This observation has also been confirmed by an empirical study where height growth was a key factor explaining species dominance (Lusk and Matus 2000). In general, model predictions were most strongly affected by model parameters describing the photosynthesis and morphology of individual trees. Thus, more detailed information on morphological parameters, as well as on physiological processes such as photosynthesis and respiration is needed in order to improve the data basis for process-based forest models.

Benefits and limitations of the modelling approach 8.2.3

Process-based models allow to investigate the implications of changes in single processes on overall system dynamics. Compared to typical gap models, which use descriptions of single-tree growth derived from statistical analyses (e.g. Bugmann 2001), FORMIND describes tree growth at the level of underlying physiological processes of photosynthesis and respiration. Thus, forest dynamics can be deduced from physiological processes and local interactions between single trees such as shading and gap creation. Moreover, the implications of management scenarios can be simulated with process-based models without relying on long-term field data. In contrast, typical gap models require a lot of data on tree growth (which are often not available) and face the problem that correlations of tree growth and light availability (or variables used as proxies for light availability) are often weak (e.g. Ong and Kleine 1996). However, the parameters of process-based models are also often unavailable and indirect methods have to be used to adjust these parameters.

The communication of the functionality of complex simulation models not only to the scientific community but also to stakeholders such as politicians, forest owners, and forest managers constitutes a great challenge (e.g. Vanclay 2003, Grimm et al. in press). During the work on this thesis, a graphical user interface was developed which allows defining management parameters and simulating different harvesting scenarios without having to deal with the source code or the definition of biological parameters. A 3D visualisation of simulation results helps to get an understanding of forest dynamics under different harvesting practices.

8.3 Conclusions and Outlook

It was the first time for tropical montane cloud forest in central Veracruz, Mexico, and Valdivian temperate rain forest in northern Chiloé Island, Chile, that a forest model was applied to study forest dynamics, productivity, and ecological impacts of harvesting strategies. The process-based forest model FORMIND proved to be able to reproduce observed forest characteristics as far as field data were available. In general, simulation results showed that both forest types have a high potential for wood production. However, every anthropogenic intervention in the form of wood extraction, even at very low levels, has an ecological impact on the forests. Comparing all logging scenarios that were investigated in this thesis, the overall ecological impact increased linearly with the amount of extracted wood. The developed ecological index, that integrates several ecological criteria, provides a first approach for the determination of management strategies serving multiple purposes such as economic income from wood production and relative maintenance of forest structure and composition to ensure the protection of non-economic ecosystem services from the native forests, e.g. soil protection, water capture, biodiversity conservation, cultural and recreation values. Moreover, simulation results serve to design management strategies that promote the regeneration of desired tree species and/or minimise shifts in the species composition of the forest.

However, a more detailed assessment of economic benefit is desirable to enhance the relevance of model results for decision makers and stakeholders that depend on the forest as a source of income. Economic extensions could include an incorporation of logging costs for different management strategies and the consideration of economic concepts such as discounting and price development. Integrated sustainability indices should be developed incorporating economic and ecological criteria which can be weighted according to preferences of stakeholders. A particular focus should be on the management of secondary forests as their area is increasing, their growth rates are high, and their structure and species composition are less vulnerable to tree harvesting than old-growth forests.

The new graphical user interface of the model provides the opportunity to use the model in workshops with decision makers, stakeholders, or students to explore implications of alternative management scenarios and to raise awareness and understanding of the underlying ecological processes of forest dynamics. Simulation exercises can support the education of forestry students with respect to the management of native forests which is often neglected in conventional curricula (e.g. Lara et al. 2003).

Process-based forest models enhance our understanding of the dynamics of species-rich moist forests and are indispensable tools to assess long-term implications of anthropogenic disturbances on forest ecosystems. Together with empirical studies, simulation approaches contribute substantially to the conservation and sustainable use of native species-rich forests outside protected areas by providing guidelines for ecologically sound management and highlighting their potential for provision of ecosystem services. During the past decade, FORMIND has been applied to study forest dynamics and implications of management activities in several forest types and regions in Southeast Asia and Latin America and model parameterisation for further study sites is ongoing. However, model parameterisation is still too labour-intensive and time-consuming to allow a standard application of FORMIND in a typical management context, although quantitative information on sustainable wood extraction rates, responses of valuable timber species to different harvesting strategies, and long-term ecological implications of wood harvesting are urgently needed for a sustainable management of forest resources in regions with high biodiversity. Thus, a comparative analysis of model parameterisations and simulation results can provide the foundation for a deeper understanding of key factors and processes that determine the dynamics of species-rich moist forests and the ecological effects of wood harvesting. On the basis of the gained insights, aggregated models should be developed that are easier to parameterise, but nevertheless facilitate the quantitative assessment of sustainable wood extraction rates and of the long-term implications of different logging strategies. Thereby such models could improve the knowledge base for a certification of sustainable forest management substantially.

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Appendix A
Description of submodels of FORMIND2.3

In the following the technical realisation of the submodels of FORMIND2.3 is described. Units of variables are given in Table A1 list of model parameters for TMCF in central Veracruz, Mexico, and VTRF in northern Chiloé Island, Chile, can be found in Tables A2 and A3, respectively.

Disturbances (only for VTRF in northern Chiloé Island, Chile)

Occasional wind throw events were modelled by removing all trees in an area comprising 2 – 4 neighbouring patches, thus creating gaps of 800 – 1600 m². The probability that a certain hectare is affected by a wind throw is 0.8% per year. Disturbance size (i.e. 2, 3, or 4 patches) is drawn from a uniform distribution.

Recruitment

If irradiance at the forest floor (I_{floor}) matches light requirements for establishment of trees of a given PFT (I_{min}, I_{max}), i.e.

$$I_{min} < I_{floor} < I_{max} \ ,$$

N_{max} small trees with a dbh of 1 cm establish. Additionally it is checked, that the height layer of seedling crowns is not completely crowded prior to establishment.

Mortality

(1) Basic mortality: Each tree has a basic PFT-specific probability to die (m_B).

(2) Size-dependent mortality: Small trees experience additional mortality (m_D) depending on their actual dbh (D),

$$m_D = \begin{cases} m_{max} - m_{max}\frac{D}{D_{mort}} & , \ if D < D_{mort} \\ 0 & , \ else \end{cases} ,$$

where m_{max} is the maximum size-dependent mortality of small trees and D_{mort} is the dbh up to which mortality is increased. Basic and size-dependent mortality are added,

$$m = m_B + m_D \, .$$

For cohorts with > 100 individuals and a dbh < 10 cm, the number of dying trees (N_d) is calculated as

$$N_d = m \cdot N_t \, ,$$

where N_t is the number of trees in the cohort; for the non-integral part of N_d it is stochastically determined if an additional tree dies. Likewise, for cohorts with < 100 individuals or dbh ≥ 10 cm it is stochastically determined if a tree dies.

(3) Self-thinning: In dense patches mortality is increased due to competition for space among the trees. When the sum of the crown area of all trees (which have their crown in this height layer) in a given height layer exceeds the patch area, trees are randomly removed until the crowns of all trees "fit" into the patch.

(4) Gap creation: Large falling trees kill a proportion of the trees in the patch where their crown hits the ground. Trees with a dbh > D_{fall} fall over with the probability p_{fall}. The probability that a tree in the target patch is killed (p_k) is proportional to the ratio between the crown projection area of the falling tree (CA) and patch size (a),

$$p_k = min\left(\frac{CA}{a}, 1\right).$$

Again, for cohorts with > 100 individuals and a dbh < 10 cm, the number of dying trees is calculated deterministically, otherwise it is stochastically determined if a tree dies. Only trees that do not overtop the falling tree by > 1 m can be killed.

Light competition

The vertical distribution of leaf area determines the light climate in each patch. This is accounted for by dividing each patch into horizontal layers of the width Δh. The crowns of most trees span over several height layers, and thus contribute to the leaf area index (LAI) in each height layer i that contains a part of the tree crown (LAI_i),

$$LAI_i = \sum_{t\ with\ crown\ in\ i} N_t \frac{CA_t}{a} \cdot LAI_t \frac{\Delta h}{CL_t},$$

with N_t being the number of trees, CA_t crown area, CL_t crown depth, LAI_t LAI of cohort t, and a patch area. When crowns of large trees exceed the patch area, "overhanging" crown and leaf area is distributed evenly to the corresponding height layers of the four neighbouring patches.

The cumulative LAI ($LAIC_i$) adds up the LAI in all height layers above layer i,

$$LAIC_i = \sum_{j>i} LAI_j.$$

The available light at the crown of each tree (I_t) is calculated via an extinction law

$$I_t = I_0 \cdot e^{-k \cdot LAIC_t},$$

with I_0 being the average irradiance above the forest canopy, $LAIC_t$ the cumulative LAI in all height layers above the crown of the tree and k the light extinction coefficient of the forest.

Growth

The calculation of light extinction within the forest canopy and leaf-level rates of photosynthesis follows Thornley and Johnson (1990) and Monsi and Saeki (1953). Both, incident irradiance and rate of photosynthesis need to be considered on the level of single leaves (i.e. per unit leaf area) and the level of an entire tree crown (per unit crown projection area), denoted by l and t respectively. The rate of single-leaf photosynthesis (P_l) is modelled as a saturating function of the incident light on the leaf (I_l),

$$P_l(I_l) = \frac{\alpha\, I_l\, p_{max}}{\alpha\, I_l + p_{max}}\,,$$

with p_{max} being the maximum rate of photosynthesis and α the initial slope of the light-response curve. The irradiance incident on the surface of a leaf within the canopy of a tree is

$$I_l = \frac{k}{1-m}\, I_t\,,$$

with I_t being the irradiance incident on the tree crown, k the light extinction coefficient of the forest, and m the light transmission coefficient of leaves. Self-shading of the tree canopy is accounted for by integrating P_l over the total LAI of tree t (LAI_t) and the resulting instantaneous rate of photosynthesis of the tree (P_t, per unit crown projection area) is

$$P_t = \int\limits_0^{LAI_t} P_l(I_l(L))dL\,,$$

where L is the cumulative LAI of the tree. Solving the integral leads to

$$P_t(I_t) = \frac{p_{max}}{k} ln \frac{\alpha\, k\, I_t + p_{max}(1-m)}{\alpha\, k\, I_t \cdot e^{-k \cdot LAIC_t} + p_{max}(1-m)}\,,$$

(Thornley and Johnson, 1990).

To calculate total annual gross biomass production of the tree (PB), the rate of photosynthesis is multiplied by the length of the photosynthetic active period per year (S), the crown area of the tree (CA), and a conversion coefficient ($codm$) from absorbed CO_2 to organic dry mass,

$$PB = P_t(I_t) \cdot S \cdot CA \cdot codm\,.$$

S is calculated as

$$S = 365 \cdot s_d\,,$$

where s_d is the average daily photosynthetic active period.

Respiration processes can be divided into growth respiration during the build-up of new biomass (parameter r_g) and maintenance respiration of living biomass (parameters r_0, r_1, r_2). Growth respiration is assumed to be a fixed fraction of net biomass production, whereas maintenance respiration is assumed to be non-linearly dependent on the living biomass (B) of the tree. Thus, biomass increment B_{inc} of the tree is calculated as

$$B_{inc} = (1 - r_g)(PB - r_0 B^{r_1})$$

for TMCF in central Veracruz or

$$B_{inc} = (1 - r_g)(PB - (r_0 B + r_1 B^2 + r_2 B^3))$$

for VTRF in northern Chiloé Island. Maintenance respiration parameters are fitted such that measured maximum diameter increment values for each PFT are reproduced. Additionally it is assured that $B_{inc}(B(D_{max})) = 0$. The new biomass ($B_{new} = B_{old} + B_{inc}$) is then translated into the new dbh of the tree via a table function. The table is filled once at the beginning of a simulation for each PFT and assigns each possible dbh (in steps of one mm) the corresponding biomass on the basis of the equation

$$B(D) = \frac{\pi}{4} D^2 \cdot H(D) \cdot \frac{f \cdot \rho}{sw},$$

with D being tree dbh, H being the height of the tree, f the form factor that corrects the deviation of the stem from the idealised conical shape, ρ the wood density and sw the fraction of stem wood biomass from total tree biomass. Between tabulated values linear interpolation is applied.

From the new dbh (sometimes converted into cm) all other variables describing the geometry of the tree are derived. Height (H) is calculated as

$$H(D) = \frac{D}{\frac{1}{h_0} + \frac{D}{h_1}}.$$

Crown depth (CL) is a constant fraction of height,

$$CL(H) = c \cdot H.$$

Crown diameter (CD) is assumed to be proportional to the stem diameter,

$$CD(D) = cd \cdot D.$$

The crown is assumed to be a cylinder, hence crown area (CA) is

$$CA(CD) = \frac{\pi}{4} CD^2.$$

LAI of a tree (LAI) is fixed to L_{max}. Stem volume (SV) is

$$SV(D) = \frac{\pi}{4} D^2 \cdot H(D) \cdot f.$$

Bole volume (stem volume below the crown, *BV*) is derived from geometrical properties of the frustum of a cone (Bronstein and Semendjajew 1991, Ditzer 1999)

$$BV(D) = \frac{1}{3f}(1 + x + x^2) \cdot (1 - CL(D)) \cdot SV(D),$$

with *x* being

$$x(D) = 1 - (1 - CL(D)) \left(\frac{3}{2} - \sqrt{3f - \frac{3}{4}} \right).$$

When all equations that are necessary to calculate the annual biomass increment of one tree are compiled together, the following lengthy expression results:

$$B_{inc} = (1-r_g)\left(\left(\frac{p_{max}}{k} ln \frac{\alpha\, k\, I_t + p_{max}(1-m)}{\alpha k I_t \cdot e^{-k \cdot LAIC_t} + p_{max}(1-m)}\right) \cdot \frac{S\, \pi\, codm}{4} \cdot \left(cd \cdot D\right)^2 - r_0 \left(\frac{\pi}{4} D^2 \cdot \frac{D}{\frac{1}{h_0} + \frac{D}{h_1}} \cdot \frac{f\, \rho}{sw}\right)^{r_1}\right).$$

Logging

(1) Selective logging: The program keeps track of harvestable trees that comply with defined criteria of the logging scenarios (e.g. commercial PFTs, minimum and maximum allowed dbh thresholds for harvesting). Before the logging module is applied, it is evaluated whether the minimum criterion (i.e. minimum number of trees to be extracted per hectare) can be fulfilled taking potential logging damages into account. If the minimum criterion is met, a logging operation takes place; otherwise logging is omitted in the respective hectare. Patches are visited randomly and the largest harvestable tree of the patch is logged, until all patches have been visited at least once or the harvest target has been met. Then, patches are visited randomly until the harvest target is met.

(2) Logging in bands: Each hectare is divided into five 20 m wide bands which are recurrently clear-cut. All trees from the logged band are removed, regardless of their PFT or dbh.

For both logging strategies, reduced impact logging is assumed. This means, that falling logged trees are directed to previously damaged patches, if possible, to reduce logging damages by falling trees. Vegetation damage in the patch where the crown of the logged tree hits the ground is simulated in the same way as described for naturally falling trees (see *Mortality* (4) Gap creation), except that harvestable trees in the target patch are prevented from being damaged. When a tree is directed to a previously damaged patch, only the difference between potential damage caused by its crown and the previously damaged proportion of the trees is damaged. Additional logging damages due to skidding apply to the entire hectare, independently of the location of logged trees. The intensity of this global damage is defined for each logging scenario depending on the logging intensity.

Variables of FORMIND2.3. **Table A1**

Variable	Description	Unit
Variables of tree cohorts		
N	Number of individuals	[1]
D	Tree diameter	[m]
H	Tree height	[m]
CD	Crown diameter	[m]
CA	Crown area	[m^2]
CL	Crown depth	[m]
B	Tree biomass	[t organic dry mass]
PB	Gross tree biomass production	[t organic dry mass]
B_{inc}	Net tree biomass production	[t organic dry mass]
SV	Tree stem volume	[m^3]
BV	Tree bole volume (volume below crown)	[m^3]
LAI	Tree leaf area index	[m^2 leaf m^{-2} ground]
P_l	Rate of photosynthesis per unit leaf area	[$\mu\mathrm{mol}(\mathrm{CO_2})\ \mathrm{m}^{-2}$leaf s^{-1}]
P_t	Rate of photosynthesis per unit ground area	[$\mu\mathrm{mol}(\mathrm{CO_2})\ \mathrm{m}^{-2}$ground s^{-1}]
I_l	Irradiance incident on leaf surface	[μmol(photons) m^{-2}leaf s^{-1}]
I_t	Irradiance incident on tree crown	[μmol(photons) m^{-2}ground s^{-1}]
Variable of height layers		
$LAIC$	Cumulative leaf area index in height layers	[m^2 leaf m^{-2} ground]
Variable of patches		
I_{floor}	Irrandiance at forest floor	[% of I_0]
Environmental variable		
S	Length of photosynthetic active period per year	[s a^{-1}]

Table A2 Parameters of FORMIND2.3 for tropical montane cloud forest in central Veracruz, Mexico. For a description of plant functional types (PFT) see Table 4.1.

Parameter	Description	Unit	PFT 1	PFT 2	PFT 3	PFT 4	PFT 5	PFT 6	Reference
Environmental parameters									
k	Light extinction coefficient	[m² ground m⁻² leaf]	0.5						Hafkenscheid (2000)
I_0	Average irradiance above canopy	[μmol(photons) m⁻² s⁻¹]	600						G. Williams-Linera (unpubl. data)
S_d	Mean sunshine hours per day	[h d⁻¹]	12						estimated
Recruitment parameters									
D_S	Diameter of ingrowing trees	[m]	0.01						technical parameter
I_{min}	Minimum light intensity for establishment	[% of I_0]	10	3	1	3	1	3	estimated
I_{max}	Maximum light intensity for establishment	[% of I_0]	100						estimated
N_{max}	Ingrowth rates of small trees	[ha⁻¹ y⁻¹]	1000	400	250	400	250	400	fitted using inventory data
Mortality parameters									
m_B	Basic mortality	[y⁻¹]	0.05	0.015	0.015	0.01	0.008	0.01	estimated
m_{max}	Maximum mortality of small trees	[y⁻¹]	0.25						estimated
D_{mort}	Diameter up to which mortality is increased	[m]	0.1						estimated
D_{fall}	Minimum diameter of falling trees	[m]	0.35						Arriaga (1987, 2000), Williams-Linera (2002)
p_{fall}	Probability of large dying trees to fall	[%]	80						Williams-Linera (2002)
Tree geometry parameters									
h_0	Parameter of diameter-height relationship	[cm m⁻¹]	2.24	2.24	2.24	2.15	2.15	2.1	Aguilar-Rodríguez et al. (2001)
h_1	Parameter of diameter-height relationship	[m]	18.55	18.55	18.55	29.26	29.26	42	

f	Form factor	[–]	0.5						Köhler (2000)
cd	Parameter of diameter-crown diameter relationship	[m cm^{-1}]	0.2						G. Williams-Linera (unpubl. data)
H_{max}	Maximum height	[m]	15	15	15	25	25	35	G. Williams-Linera (pers. observation)
D_{max}	Maximum diameter	[m]	0.35	0.35	0.35	0.8	0.8	1.0	
c	Crown length fraction	[–]	0.1						estimated
L_{max}	Maximum leaf area index per tree	[m^2 leaf m^{-2} ground]	2						estimated
sw	Fraction of stem wood biomass to total biomass	[–]	0.7						Köhler (2000)
Biomass production parameters									
p_{max}	Maximum rate of photosynthesis	[µmol(CO$_2$) m^{-2} s^{-1}]	20	16	10	16	10	16	Ellis et al. (2000), Dillenburg et al. (1995)
α	Slope of light-response-curve	[µmol(CO$_2$) µmol(photons)$^{-1}$]	0.15	0.2	0.25	0.2	0.25	0.2	estimated
ρ	Wood density	[t m^{-3}]	0.55	0.65	0.7	0.65	0.7	0.65	Bárcenas et al. (1998), Aguilar-Rodríguez et al. (2001)
r_g	Parameter of growth respiration	[–]	0.2						Ryan (1991)
r_0	Parameter of maintenance respiration	[–]	0.79	0.59	0.41	0.3	0.19	0.23	fitted using diameter increment data (Williams-Linera 1996)
r_1			1.2	1.2	1.2	1.07	1.1	1.02	
m	Transmission coefficient of leaves	[–]	0.1						Larcher (2001)
$codm$	Parameter for conversion in organic dry matter	[t µmol(CO$_2$)$^{-1}$]	0.63 44e^{-12}						Larcher (2001)
Technical parameters									
a	Patch size	[m^2]	400						technical parameter
Δh	Width of horizontal discretisation	[m]	0.5						technical parameter

Table A3 Parameters of FORMIND2.3 for Valdivian temperate evergreen rain forest in northern Chiloé Island, Chile. AP = *Aextoxicon punctatum*, EC = *Eucryphia cordifolia*, LP = *Laureliopsis philippiana*, MY = *myrtaceous species*.

<table>
<tr><th>Parameter</th><th>Description</th><th>Unit</th><th>AP</th><th>EC</th><th>LP</th><th>MY</th><th>Reference</th></tr>
<tr><td colspan="8">Environmental parameters</td></tr>
<tr><td>k</td><td>Light extinction coefficient</td><td>[m^2 ground m^{-2} leaf]</td><td colspan="4">0.5</td><td>estimated</td></tr>
<tr><td>I_0</td><td>Average irradiance above canopy</td><td>[µmol(photons) m^{-2} s^{-1}]</td><td colspan="4">700</td><td>C. Lovengreen (unpubl. data)</td></tr>
<tr><td>S_d</td><td>Mean sunshine hours per day</td><td>[h d^{-1}]</td><td colspan="4">12</td><td>estimated</td></tr>
<tr><td colspan="8">Recruitment parameters</td></tr>
<tr><td>D_S</td><td>Diameter of ingrowing trees</td><td>[m]</td><td colspan="4">0.01</td><td>technical parameter</td></tr>
<tr><td>I_{min}</td><td>Minimum light intensity for establishment</td><td>[% of I_0]</td><td>1</td><td>70</td><td>3</td><td>1</td><td>Lusk and Kelly (2003)</td></tr>
<tr><td>I_{max}</td><td>Maximum light intensity for establishment</td><td>[% of I_0]</td><td>90</td><td>100</td><td>70</td><td>95</td><td>estimated</td></tr>
<tr><td>N_{max}</td><td>Maximum recruitment rates of small trees</td><td>[ha^{-1} y^{-1}]</td><td>100</td><td>75</td><td>250</td><td>150</td><td>estimated</td></tr>
<tr><td colspan="8">Mortality parameters</td></tr>
<tr><td>m_B</td><td>Basic mortality</td><td>[y^{-1}]</td><td>0.0045</td><td>0.005</td><td>0.0035</td><td>0.0025</td><td>estimated</td></tr>
<tr><td>m_{max}</td><td>Maximum mortality of small trees</td><td>[y^{-1}]</td><td colspan="4">0.055</td><td>estimated</td></tr>
<tr><td>D_{mort}</td><td>Diameter up to which mortality is increased</td><td>[m]</td><td colspan="4">0.15</td><td>estimated</td></tr>
<tr><td>D_{fall}</td><td>Minimum diameter of falling trees</td><td>[m]</td><td colspan="4">0.45</td><td>estimated</td></tr>
<tr><td>p_{fall}</td><td>Probability of dying trees to fall</td><td>[%]</td><td colspan="4">30</td><td>estimated</td></tr>
<tr><td colspan="8">Tree geometry parameters</td></tr>
<tr><td>h_0</td><td>Parameter of diameter-height relationship</td><td>[cm m^{-1}]</td><td colspan="4">1.2</td><td>Brun (1969)</td></tr>
<tr><td>h_1</td><td>Parameter of diameter-height relationship</td><td>[m]</td><td>41.6</td><td>48.7</td><td>40.1</td><td>27.7</td><td>Brun (1969)</td></tr>
</table>

f	Form factor	[–]	0.4	0.4	0.4	0.35	Brun (1969)
cd	Parameter of diameter-crown diameter relationship	[m cm^{-1}]	0.12				estimated
H_{max}	Maximum height	[m]	30	40	30	20	e.g. Brun (1969),
D_{max}	Maximum diameter	[m]	1	2	1	0.7	Lusk and del Pozo (2002)
c	Crown depth fraction	[–]	0.25				estimated
L_{max}	Maximum leaf area index per tree	[m^2 leaf m^{-2} ground]	4				Saldaña and Lusk (2003)
sw	Fraction of stem wood biomass to total biomass	[–]	0.7				estimated
Biomass production parameters							
p_{max}	Maximum rate of photosynthesis	[µmol(CO$_2$) m^{-2} s^{-1}]	5.6	10	6.4	7	C. Lusk (unpubl. data) and estimated
α	Slope of light-response-curve	[µmol(CO$_2$) µmol(photons)$^{-1}$]	0.25	0.2	0.2	0.35	estimated
ρ	Wood density	[t m^{-3}]	0.59	0.72	0.55	1.15	Pérez-Galaz (1983), Diaz-vaz et al. (2002)
r_g	Parameter of growth respiration	[–]	0.2				Ryan (1991)
r_0			0.1	0.11	0.13	0.1	estimated using
r_1	Parameter of maintenance respiration	[–]	0.0	0.0	0.0008	0.003	diameter increment data
r_2			0.0001	0.0	0.0	0.0	(Gutiérrez et al., in prep.)
m	Transmission coefficient of leaves	[–]	0.1				Larcher (2001)
$codm$	Parameter for conversion in organic dry matter	[t µmol(CO$_2$)$^{-1}$]	0.63 44e^{-12}				Larcher (2001)
Technical parameters							
a	Patch size	[m^2]	400				technical parameter
Δh	Width of horizontal discretisation	[m]	0.5				technical parameter

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Appendix B

List of tree species in tropical montane cloud forest in central Veracruz, Mexico

Table B1 List of tree species in five study sites in tropical montane cloud forest in central Veracruz, Mexico (Williams-Linera, unpubl. data).

Species	PFT
Acacia pennatula	1
Annona cherimola	2
Arachnothryx capitellata	1
Beilschmiedia mexicana	5
Brunellia mexicana	1
Carpinus caroliniana	2
Celestraceae	2
Cinnamomun effusum	3
Clethra mexicana	6
Cleyera theioides	5
Compositae	1
Drimys granadensis	3
Eugenia mexicana	3
Eugenia xalapensis	3
Fagus grandifolia	6
Heliocarpus donnell-smithii	1
Ilex beliziensis	3
Ilex tolucana	5
Inga flexuosa	1
Lauraceae	3
Liquidambar styraciflua	6
Lonchocarpus guatemalensis	6
Magnolia schiedeana	5
Miconia glaberrima	2
Mollinedia viridiflora	3
Myrsinaceae	2
Nectandra losenerii	5
Oreopanax xalapensis	2
Ostrya virginiana	3
Palicourea padifolia	2
Perrottetia ovata	2
Persea americana	6
Pithecellobium arboreum	4
Podocarpus matudai	5
Prunus samydoides	3
Quercus acutifolia	4
Quercus germana	6
Quercus insignis	6
Quercus leiophylla	4
Quercus sartorii	6
Quercus salicifolia	4
Quercus xalapensis	5
Rapanea myricoides	1
Rhamnus capraeifolia	2
Rubiaceae	2
Saurauia scabrida	2
Saurauia leucocarpa	2
Solanaceae	1
Solanum nigricans	1
Styrax glabrescens	2
Ternstroemia sylvatica	3
Tree fern	2
Turpinia insignis	2
Vaccinium leucanthum	2
Viburnum microcarpum	2
Weinmannia pinnata	2
Zanthoxylum clava-herculis	2
Zanthoxylum mayanum	2

ZUSAMMENFASSUNG

Trotz ihrer herausragenden Bedeutung für die Erhaltung von biologischer Vielfalt, die Regulierung regionaler Wasserkreisläufe und des globalen Klimas sind artenreiche Feuchtwälder weltweit von Abholzung und Umwandlung in Weideland, landwirtschaftliche Nutzflächen, urbane Gebiete oder Plantagen exotischer Baumarten bedroht. Eine nachhaltige Nutzung dieser Wälder wird zusätzlich durch fehlendes Verständnis der Walddynamik und der langfristigen Auswirkungen von verschiedenen Nutzungsstrategien erschwert. Diese Arbeit hat zum Ziel, zu einem besseren Verständnis der natürlichen Walddynamik beizutragen sowie die Produktivität der Wälder unter verschiedenen Nutzungsszenarien zu untersuchen und deren ökologischen Auswirkungen zu quantifizieren. Durch die quantitative und langfristige Analyse von Nutzungsszenarien legt diese Arbeit die Grundlagen für eine nachhaltige Nutzung artenreicher Feuchtwälder.

Der Untersuchungsgegenstand dieser Arbeit sind tropische Bergnebelwälder in Zentral-Veracruz in Mexiko und temperierte Valdivianische Regenwälder im Norden der Insel Chiloé in Chile. Beide Waldtypen beherbergen eine herausragende biologische Vielfalt und haben eine große Bedeutung für die Bereitstellung von Ökosystemdiensten wie z.B. Wasseraufnahme aus Nebel, Erhaltung der Wasserqualität von Flüssen und Seen, Erosionsschutz der Böden, Klimaregulierung und Speicherung von Kohlenstoff. Trotzdem hat ihre Fläche in der Vergangenheit durch Umwandlung in andere Landnutzungsformen stark abgenommen. Ihre natürliche Walddynamik ist kaum bekannt, und Konzepte für eine nachhaltige Nutzung der artenreichen Wälder fehlen weitgehend. In Zentral-Veracruz, Mexiko, kommt der Großteil des Brennholzes zum Kochen und Heizen aus Fragmenten von Altbeständen des Bergnebelwalds. Quantitative Informationen über nachhaltige Holzentnahmemengen und langfristige ökologische Konsequenzen sind nicht vorhanden. Sekundärwälder, die nach der Aufgabe anderer Landnutzungen nachwachsen, spielen eine immer größere Rolle für die Bereitstellung von Ökosystemdienstleistungen. Daher sind die spezifischen Zielstellungen bezüglich der Bergnebelwälder in Zentral-Veracruz, die natürliche Waldregeneration hinsichtlich des Potenzials der Wälder, Ökosystemdienste zu leisten, zu simulieren und die langfristigen Auswirkungen einer wiederholten selektiven Holzentnahme auf Waldstruktur und Artenzusammensetzung zu untersuchen. Die Valdivianischen Urwälder in Südmittelchile sind stark von einer Umwandlung in Plantagen exotischer Baumarten bedroht. Ihre Dynamik ist noch nicht sehr gut untersucht und es ist wenig Erfahrung mit ihrer Nutzung vorhanden. Deshalb hat diese Arbeit zum Ziel, zu einem besseren Verständnis ihrer Dynamik unter verschiedenen Störungsregimes beizutragen und sowohl ihre Produktivität unter verschiedenen Nutzungsszenarien als auch deren ökologische Auswirkungen zu untersuchen.

Um diese Fragen zu untersuchen, wurde das prozessbasierte Waldmodell FORMIND angewandt. FORMIND ist ein individuen-orientiertes Waldmodell, das die Kohlenstoffbilanz für jeden Baum abhängig vom Lichtklima im Wald berechnet. Daher ermöglicht FORMIND eine Untersuchung von Nutzungsszenarien, die sich in den bevorzugten Baumarten, -größen und der Nutzungsintensität unterscheiden. Um das Modell an die zwei Untersuchungsregionen anzupassen, wurden die vorkommenden Baumarten nach ihrem Lichtbedürfnis und ihrer maximalen Höhe in funktionelle Typen unterteilt. Für jeden funktionellen Typ wurden auf der Grundlage von Literaturangaben, Daten aus den Untersuchungsgebieten und Expertenschätzungen Regenerations-, Wachstums- und Mortalitätsparameter sowie allometrische Funktionen der Baumgeometrie bestimmt. Das Modell wurde getestet, indem Modellvorhersagen mit Felddaten auf der Einzelbaumebene, der Ebene der funktionellen Typen und der Ebene der gesamten Baumgemeinschaft verglichen wurden.

Die Simulationsergebnisse zeigten, dass mexikanischer Bergnebelwald nach großflächigen Störungen oder der Aufgabe vorhergehender Landnutzung schnell regeneriert. Aggregierte Waldeigenschaften, zum Beispiel Gesamtstammanzahl und -stammgrundfläche, erreichten Werte eines Primärwaldes nach ca. 80 Jahren. Der Blattflächenindex und die Waldhöhe, die für die Bereitstellung von Ökosystemdiensten, zum Beispiel der Wasseraufnahme aus Nebel und den Erosionsschutz, eine wichtige Funktion haben, hatten spätestens nach 40 – 80 Jahren annähernd Werte eines Primärwaldes erreicht. Waldeigenschaften, die auf die Ähnlichkeit der Artenzusammensetzung mit Primärwäldern hinweisen, benötigten längere Zeitspannen für ihre Erholung. Die Anzahl der großen alten Bäume und der Anteil der Stammgrundfläche der verschiedenen funktionellen Typen erreichten Werte eines Primärwaldes nach 150 bzw. 300 Jahren.

Die Simulation von wiederholter Brennholzentnahme aus mexikanischem Bergnebelwald zeigte, dass sich die Waldstruktur mit steigender Menge entnommenen Holzes zunehmend vereinheitlichte und die Wälder „jünger“ wurden, weil die Anzahl großer, alter Bäume stark abnahm, während die Anzahl der Bäume in niedrigen Durchmesserklassen anstieg. Die Artenzusammensetzung verschob sich zugunsten von funktionellen Typen, die nicht als Brennholz genutzt werden. Diese Veränderungen können sich über einen Zeitraum von einigen Jahrzehnten bis zu mehr als hundert Jahren erstrecken. Dem Wald kann ein Holzvolumen von bis zu 12 m^3/ha pro Jahr entnommen werden. In Teilen des Untersuchungsgebietes scheint die Brennholzentnahme an der Grenze dieser nachhaltigen Nutzungsrate zu liegen.

Verglichen mit dem mexikanischen Bergnebelwald hat der Valdivianische Regenwald in Südmittelchile eine langsamere Dynamik. Gesamtstammanzahl und -grundfläche erreichten einen Fließgleichgewichtswert nach 100 bzw. 200 Jahren. Die ersten 400 Jahre der Sukzession dominierte bezüglich der Stammgrundfläche die lichtliebende *Eucryphia cordifolia*, die später durch schattentolerante Arten verdrängt wurde. Ohne größere Störungen, z.B. Windwürfe, tendierte *E. cordifolia* dazu, nach ca. 800 Jahren vollständig zu verschwinden. Wurden größere Störungen einbezogen, blieb *E. cordifolia* in Form von wenigen großen Individuen erhalten, die einen großen Teil der Stammgrundfläche stellten. Die Stammgrundfläche der verschiedenen Arten erreichte erst ca. 1000 Jahre nach dem Beginn der Sukzession ein Gleichgewicht.

Die Simulation von potenziellen Nutzungsszenarien für Valdivianischen Regenwald zeigte, dass Kahlschläge in 20-m breiten Streifen die höchsten Erträge erzielten, weil sie die Regeneration der schnellwachsenden *E. cordifolia* förderten. Dem Wald konnte ein Holzvolumen von bis zu 13 m^3/ha pro Jahr entnommen werden. Diese hohen Erträge wurden aber auf Kosten einer starken Veränderung der Waldstruktur und Artenzusammensetzung erzielt. Demgegenüber erhielt eine Einzelbaumnutzung die strukturelle Komplexität und Artenzusammensetzung eines alten Waldes besser und begünstigte die Regeneration von schattentoleranten Baumarten. Die Erträge von bis zu 7.5 m^3/ha pro Jahr waren jedoch geringer.

Für beide Waldtypen wurde im Rahmen dieser Arbeit zum ersten Mal ein Waldmodell angewandt, um Walddynamik, Produktivität und ökologische Auswirkungen von Nutzungsszenarien zu untersuchen. FORMIND erwies sich als imstande, beobachtete Waldeigenschaften zu reproduzieren soweit Felddaten verfügbar waren. Für mexikanischen Bergnebelwald in Zentral-Veracruz waren Felddaten aus einer Chronosequenz-Studie vorhanden, die eine Validierung des Modells ermöglichten. Das Modell simulierte die qualitative Entwicklung aggregierter Waldeigenschaften korrekt, obwohl das Einzelbaumwachstum leicht überschätzt und damit die Regenerationszeit des Waldes leicht unterschätzt wurde. Eine umfangreiche Sensitivitätsanalyse zeigte, dass die Modellergebnisse stark von Parametern beeinflusst wurden, die die Photosynthese und Morphologie von Einzelbäumen beschreiben. Den stärksten Einfluss hatte der Parameter, der den linearen Zusammenhang zwischen Stamm- und Kronendurchmesser beschreibt. Detailliertere Informationen über morphologische und physiologische Parameter könnten also die Datengrundlage für prozessbasierte Waldmodelle erheblich verbessern.

Im Allgemeinen zeigten die Simulationsergebnisse, dass beide Waldtypen ein großes Nutzungspotenzial haben. Allerdings hat jeder anthropogene Eingriff in Form von Holzentnahme, auch bei geringen Mengen, ökologische Folgen für den Wald. Vergleicht man alle Nutzungsszenarien, die im Rahmen dieser Arbeit simuliert wurden, dann steigen die ökologischen Auswirkungen linear mit der entnommenen Holzmenge an. Die Simulationsergebnisse ermöglichen es also, Nutzungsstrategien zu definieren, die Naturschutz und Holzproduktion entsprechend der Präferenzen der Waldbesitzer oder anderer Interessenvertreter in geeigneter Weise verbinden. Zusätzlich erlauben es die Simulationsergebnisse, Nutzungsstrategien zu konzipieren, die die Regeneration erwünschter Baumarten fördern oder Verschiebungen der Artenzusammensetzung minimieren. In allen Nutzungsszenarien ging die Anzahl der großen, alten Bäume drastisch zurück. Da sie wichtige Lebensräume für viele hoch spezialisierte Tier- und Pflanzenarten bereitstellen, sollten einige große alte Bäume explizit im Bestand belassen werden.

Prozessbasierte Waldmodelle tragen zu einem besseren Verständnis der Dynamik artenreicher Wälder bei und sind wertvolle Werkzeuge, um langfristige Auswirkungen anthropogener Eingriffe auf Waldökosysteme abzuschätzen. Zusammen mit empirischen Untersuchungen leisten Modellierungsansätze einen unverzichtbaren Beitrag zur Erhaltung und nachhaltigen Nutzung von natürlichen artenreichen Wäldern außerhalb von Schutzgebieten, indem sie Managementempfehlungen für eine ökologisch nachhaltige Nutzung geben und das Potenzial der Wälder zur Leistung von Ökosystemdiensten aufzeigen.

RESUMEN

A pesar de la reconocida importancia de los bosques lluviosos ricos en especies para la conservación de la biodiversidad, la regulación regional de los ciclos hidrológicos y el clima global, éstos están en peligro a nivel mundial por la conversión a praderas, tierras agrícolas, áreas urbanas o plantaciones de especies exóticas. El manejo sustentable de estos bosques está obstaculizado por el insuficiente conocimiento de su dinámica y la respuesta en largo plazo a las distintas estrategias de cortas que se les aplican. Esta tesis contribuye al mejor entendimiento de la dinámica natural de estos bosques, explorando la productividad de bosques nativos sujetos a distintas estrategias de manejo y cuantificando sus impactos ecológicos. A través del análisis cuantitativo de los efectos a largo plazo de las estrategias de corta, se entregan los fundamentos para el manejo sustentable de bosques lluviosos multiespecíficos.

Esta tesis se focaliza en dos áreas de estudio: los bosques nublados de montaña del trópico (TMCF) en Veracruz central, México, y en los bosques templados valdivianos (VTRF) en el norte de la Isla de Chiloé, Chile. Ambos tipos de bosques son reconocidos por su excepcional biodiversidad y su importancia en la provisión de servicios ecosistémicos, tales como la captura agua proveniente de las nubes, calidad de agua y protección del suelo, regulación climática, almacenamiento de carbono, etc. En Veracruz central, México, la extracción de leña para calefacción y cocinas proviene de TMCF fragmentados. Sin embargo, no hay información cuantitativa de los límites de corta para un manejo sustentable y de las consecuencias ecológicas en largo plazo de una extracción repetitiva de leña. En Veracruz central, los bosques secundarios establecidos luego del abandono del uso de tierra (agrícola o ganadero) son cada vez más importantes por el rol que prestan para proveer servicios ecosistémicos. Por lo tanto, los objetivos específicos concernientes a los TMCF de Veracruz central son simular la regeneración natural del bosque con respecto al potencial del bosque para proveer servicios ecosistémicos e investigar los impactos en el largo plazo de la corta selectiva de baja intensidad en la estructura del bosque y su composición. Los bosques valdivianos vírgenes de Chile centro sur están severamente en peligro por la conversión a plantaciones monoespecíficas de especies exóticas. La dinámica forestal es aun no bien entendida y hay muy poca experiencia respecto a su manejo. Así, los objetivos específicos concernientes a los VTRFs son el estudio en el largo plazo de la dinámica forestal bajo distintos regímenes de disturbio como también la exploración de su productividad e impactos ecológicos de distintas estrategias de manejo.

Para abordar estas preguntas, se aplicó un modelo de crecimiento de bosques basado en procesos llamado FORMIND. FORMIND es un modelo forestal orientado en el individuo que calcula el balance de carbono de cada árbol en base a la disponibilidad de luz

dentro del bosque. De esta forma, FORMIND permite una incorporación detallada de las diferentes estrategias de corta sobre grupos de especies objetivo y tamaños de árboles, o la aplicación de distintas intensidades de corta. Para adaptar FORMIND a las dos áreas de estudio, las especies arbóreas fueron agrupadas en tipos funcionales (PFTs) de acuerdo a sus necesidades de luz y a su altura máxima. Para cada PFT fueron ajustados parámetros de regeneración, crecimiento y mortalidad como también fueron definidas relaciones alométricas de la geometría del árbol. El desempeño del modelo fue testeado comparando las predicciones del modelo con datos de terreno a nivel de árboles individuales, PFTs y la comunidad arbórea completa.

Los resultados de la simulación sugieren que la regeneración es rápida en los TMCFs después de disturbios de gran escala o en terrenos abandonados. Las características agregadas del bosque tales como densidad total de tallos y área basal total alcanzaron valores de un bosques maduro luego de aproximadamente 80 años. El índice de área foliar y la altura del bosque, los cuales son indicadores importantes de la habilidad del bosque para proveer servicios ecosistémicos (tales como captura de agua desde las nubes, protección del suelo) se recuperan luego de aproximadamente 40 – 80 años. Otras características del bosque que indican la similaridad de la composición de especies con las condiciones de un bosque maduro, requieren mayor tiempo para ser recuperadas. Tanto el número de árboles grandes y longevos como el área basal de los diferentes PFTs alcanzan, respectivamente, valores de bosque maduro luego de 150 años y 300 años después de comenzar la sucesión.

Las simulaciones de obtención de leña desde TMCF muestra que la extracción repetida puede ser hasta 12 m^3/ha por año. Aumentos en las cantidades extraídas implican una simplificación en la estructura del bosque, el cual se transforma en un bosque “joven” debido a la desaparición de árboles longevos y grandes, como también al incremento de árboles en las clases de diámetro pequeñas. La composición de especies cambia hacia especies arbóreas que no son cosechadas para leña. Estos cambios pueden tomar algunas décadas hasta más de cien años. Al menos en parte de la región de estudio, la extracción de leña estaría sobrepasando la capacidad regenerativa del bosque.

En comparación con los TMCFs en México, la dinámica de los VTRFs en Chile es lenta. Las densidades totales de árboles se estabilizan después de 100 años y el área basal total luego de 200 años. Los primeros 400 años de sucesión son dominados por *Eucryphia cordifolia*, especie intolerante a la sombra, la cual es reemplazada posteriormente por especies sombra tolerantes. En ausencia de disturbios de tamaños intermedios, tales como tormentas de viento, *E. cordifolia* tiende a desaparecer luego de aproximadamente 800 años. Cuando disturbios naturales de tamaño intermedio son incorporados en el modelo, *E. cordifolia* es mantenido en el bosque donde pocos individuos grandes de *E. cordifolia* acumulan una gran proporción del área basal del rodal. El área basal de las diferentes especies continua cambiando por alrededor de 1000 años luego de comenzada la sucesión.

Las simulaciones de estrategias potenciales de cosecha para VTRF muestran que cortas en fajas de 20 m de ancho generan la mas alta productividad alcanzando 13 m^3/ha por año dado que promueve la regeneración de *E. cordifolia*, una especie de relativamente rápido crecimiento. Sin embargo, estos altos niveles de cosecha son acompañados por una fuerte alteración de la estructura y composición del bosque. En contraste, la corta selectiva provee menor productividad, pero mejor conserva las características de un bosque maduro y favorece la regeneración de especies tolerantes a la sombra.

Para ambos tipos de bosque, es la primera vez que un modelo forestal es aplicado para estudiar la dinámica, productividad e impactos ecológicos de las estrategias de cortas en el bosque. En general, FORMIND fue capaz de reproducir las características observadas en el bosque por medio de datos de terreno. Para el bosque TMCF en México, fue posible validar el modelo con datos empíricos de regeneración usando una cronosecuencia sucesional. El modelo predijo correctamente el desarrollo de las características agregadas del bosque, aunque sobreestimo levemente el crecimiento de árboles individuales y consecuentemente subestimó el tiempo de recuperación del bosque. Un análisis extensivo de sensibilidad reveló que las predicciones del modelo fueron mas fuertemente afectadas por parámetros del modelo que describen la fotosíntesis y la morfología de los árboles individuales, especialmente el parámetro de relación lineal entre el diámetro del tallo y el diámetro de la copa. Entonces, se requiere información mas detallada sobre parámetros morfológicos, como también sobre procesos fisiológicos tales como fotosíntesis y respiración, para así mejorar la base de datos para la estimación de parámetros de modelos forestales basados en procesos.

En general, los resultados de simulación muestran que ambos tipos forestales tienen un alto potencial para la producción de madera. Sin embargo, cada intervención antropogénica en la forma de extracción maderera, aun en pequeñas cantidades, tiene un impacto ecológico sobre el bosque. Comparando todos los escenarios de cortas que fueron investigados en esta tesis, los impactos ecológicos aumentaron linealmente con la cantidad de madera extraída. Así, los resultados de simulación son útiles para definir un tipo de manejo que balancee los objetivos de producción con los de conservación de acuerdo a las preferencias de los tomadores de decisiones. Además, las estrategias de manejo pueden ser diseñadas para promover la regeneración de una especie arbórea deseada y/o minimizar los cambios en la composición de especies del bosque. Algunos árboles grandes y longevos debieran ser explícitamente dejados en el rodal dado que proveen un importante hábitat para muchas especies de plantas y animales. La mayoría de los escenarios de corta fallan en mantenerlos.

Los modelos forestales basados en procesos realzan nuestro entendimiento de la dinámica de bosque húmedos ricos en especies y son herramientas valiosas para explorar las implicancias en el largo plazo de los disturbios antropogénicos en los ecosistemas forestales. Junto con el desarrollo de estudios empíricos, las aproximaciones por medio de la simulación generan una contribución indispensable para la conservación y el uso sustentable de bosques ricos en especies nativas fuera de áreas protegidas. Estos estudios proveen una guía para el manejo ecológicamente sustentable y resaltan su potencial para la provisión de servicios ecosistémicos.

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