AN ABSTRACT OF THE THESIS OF

Carlos Alberto Sierra for the degree of Master of Science in Forest Science presented on March 20, 2006.
Title: Spatial and Temporal Variability of Carbon Dynamics in a Tropical Forest of Colombia

Abstract approved:

Mark E. Harmon

Despite the importance of tropical forest ecosystems in the global carbon cycle, there have been few studies of carbon dynamics in this biome. The magnitude of carbon stocks in the tropics and their changes over time are poorly known since ground-based observations are lacking. In this study, total carbon stocks (TCS) and net ecosystem production (NEP) were quantified for tropical forests of the Porce region of Colombia. A modeling exercise was also performed to analyze the effects of population and community processes on carbon dynamics at the ecosystem level.

A set of 110 permanent plots were used to estimate TCS and its uncertainty in primary and secondary forests. In primary forests, mean TCS were estimated to be 383.7 ± 43.0 Mg C ha^{-1} (± standard error). Of this amount, soil organic carbon to 4 m depth represented 59%, total aboveground biomass 29%, total belowground biomass 10%, and necromass 2%. In secondary forests, TCS was 228.2 ± 11.5 Mg C ha^{-1}. Of this store, soil organic carbon to 4 m depth accounted for 84%, total aboveground biomass represented only 9%, total belowground biomass 5%, and total necromass 1%. Based on the uncertainty analysis of TCS estimates, the variability associated with the spatial variation

of C pools between plots was higher than measurement errors within plots. A larger variability was observed in primary than in secondary forests and this difference might be explained by gap dynamics.

Net ecosystem production was measured in primary forests in a set of 33 permanent plots from 2000 to 2002 in two, one-year intervals. Uncertainty analysis indicated that NEP ranged between -4.03 and 2.22 Mg C ha^{-1} yr^{-1} for the two intervals. This range was compared to *a priori* defined range of natural variation (-1.5 and 1.5 Mg C ha^{-1} yr^{-1}) estimated from the ecosystem model STANDCARB. The observed variation in NEP did not provide sufficient evidence to reject the hypothesis that the ecosystem was within its expected natural range.

Simulations using the STANDCARB model showed that at the population level, the processes of colonization and mortality can limit the maximum biomass achieved during a successional sequence. Colonization can introduce lags during the initiation of succession and mortality can have important effects on annual variation in carbon stores. Community dynamics, defined as the replacement of species during succession, altered the mixture of species over time. When species had different ecosystem parameters, such as growth and mortality rates, community dynamics caused non-linear patterns of carbon accumulation. These patterns could not be reproduced using a single species with the average of parameters of a multi-species simulation or by using the more abundant species in the simulations.

Spatial and Temporal Variability of Carbon Dynamics in a Tropical Forest of Colombia

by

Carlos Alberto Sierra

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirement for the
degree of

Master of Science

Presented on March 20, 2006

Commencement June 2006

Master of Science thesis of Carlos Alberto Sierra presented on March 20, 2006.

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Carlos Alberto Sierra, Author

ACKNOWLEDGEMENTS

I want to expresses my sincere appreciation to Mark E. Harmon, my major professor, for his continuous support, encouragement, and intellectual stimulation. I remain grateful to him for taking me on as student in the first place, for offering support in adapting to the American culture, for proving a warm and friendly atmosphere to work in, and for the good jams we had playing music.

I would also like to thank Elizabeth Sulzman and David Turner for serving as committee members. They provided invaluable advice during different stages of the development of this thesis.

I owe especial gratitude to Jorge I. del Valle and Sergio Orrego for providing me the opportunity to join their research group back in 1999, for providing a very stimulating research atmosphere during my undergraduate work, and for allowing me to further my academic inquiries by providing a wealth of data. I am also grateful to Flavio Moreno for thoughtful discussions, for encouragement to pursue a graduate degree, and for sharing his hard won data.

I am indebted to my different sources of funding in the US and Colombia: The Eduardo Ruiz Landa Founders Fellowship, OSU Foundation Fellowship Tuition Support Scholarship, the Ward K. Richardson Family Forestry Faculty Endowment, H. J. Andrews LTER (DEB-0218088), Pacific Northwest Experiment Station, Universidad Nacional de Colombia Sede Medellín, and Empresas Públicas de Medellín E.S.P. (contract, 3/DJ1367/17 Acta 19). In particular, I want to express a deep gratitude to

Wayne and Beverly Gaskins for their generosity establishing the Eduardo Ruiz Landa Founders Fellowship.

This thesis was greatly benefited by informal but thoughtful discussions with Manuela Huso and Hank Loescher, special thanks to them. I was also benefited by close collaboration with my fellow graduate students. Thanks to Joselin Matkins, Jessica Halofsky, Alison Cross, Travis Woolley, Tiffany Van Huysen, and all the fellows in the computer lab who contributed in many different ways to the completion of this work.

Thanks to all my family in Colombia and Argentina for their support, understanding, and love. I never would accomplish my career goals without their soulful companionship.

Thanks to my father and my sister for bringing new members to my family. The kids provided a lot of emotional inspiration.

Thanks to my friends for helping me in preserving my mental health, especially my friends in Corvallis for countless hours of fun at the few local bars. Also, special thanks to my friends in Colombia, for all the good times and their unconditional friendship.

Finally, I want to express profound gratitude to my beloved friend Adriana Mosquera, who left the physical world to remain utterly present in my thoughts.

CONTRIBUTION OF AUTHORS

Dr. Mark E. Harmon was involved in the design, analysis, and writing of each manuscript. Jorge I. del Valle and Sergio Orrego were involved in the design and establishment of the permanent plots. Flavio Moreno provided information on soil carbon to 4 m depth, soil respiration, litterfall, decomposition, and root production. Mauricio Zapata and Gabriel Colorado provided aboveground biomass equations. Maria A. Herrera provided estimations of biomass in herbaceous and non-woody vegetation, and litter stocks. David E. Restrepo contributed with biomass equations for palms. Wilson Lara provided estimations of soil organic carbon. Lina Loaiza and Lina Berrouet provided estimations of land cover areas. Freddy Benjumea provided data on coarse root biomass. During the field campaign, Carlos A. Sierra participated in the establishment of permanent plots, developed root biomass equations in secondary forests, measured fine root biomass in primary and secondary forests, and fine root production in secondary forests.

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Spatial and temporal variability of carbon dynamics in a tropical forests of Colombia

CHAPTER 1

INTRODUCTION

Carlos A. Sierra

Human activities are causing important modifications to global climate and biodiversity through land transformations, modifications of biogeochemical cycles, and biotic exchange (Vitousek et al. 1997). One of the most important human driven changes is the modification of the global carbon cycle (Falkowski et al. 2000). Fossil fuel combustion and tropical deforestation have been the main causes of the observed increase of CO_2 in the atmosphere during the last century, driving important climatic modifications (IPCC 2001). Global circulation models predict increases in global temperature in the range 1.4-5.8 ºC for the end of the 21st century as a result of continued increases in atmospheric CO_2 concentrations. The consequences of this global warming are uncertain and may have large costs for society. For this reason important efforts have been made in science (e.g. IPCC 2001) and policy (Carabias 2002) to understand, predict, and mitigate climate change.

Tropical forests play an important role in the C cycle. The tropics, as a biome, account for the highest C stock (340 Pg C) and Net Primary Production (21.9 Pg C yr^{-1}) of the globe (Chapin et al. 2002). However, tropical deforestation also emits approximately 0.96-2.11 Pg C yr^{-1} (Achard et al. 2002, Houghton 2003). These numbers are rough estimates and detailed quantifications of carbon stocks, sources, and sinks have yet to be estimated (Clark 2004). It is well recognized that the net flux of carbon from terrestrial ecosystems to the atmosphere is uncertain. However, the uncertainties are higher in the tropics than in mid- and high-latitudes because there are few monitoring sites and this region's atmospheric transport is not well understood (Houghton 2003). A better

assessment of C dynamics in the tropics would therefore strengthen understanding of the global C cycle.

In the political arena, the United Nations Convention on Climate Change (UNFCCC) has proposed the establishment of new forests in developing countries to sequester C and mitigate global warming (Art. 12, Kyoto Protocol). The so-called Clean Development Mechanism (CDM), defined in the Kyoto Protocol, is a tool that allows developed countries to invest in forestry projects in developing countries to achieve their greenhouse-gas-reduction targets. About $16.1 billion could be invested in reforestation of degraded lands in the period 2008-2012 (Niles et al. 2001), which could promote the recovery of deforested tropical lands and ameliorate biodiversity extinction rates. However, uncertainties in methods for C flux quantification could constrain the capacity of developing countries to formulate successful C sequestration projects. Therefore, advancing the understanding of C dynamics in tropical forests has high relevance in science and policy.

In this thesis I present estimates of total carbon stocks in a heterogeneous landscape in the Porce Region of Colombia (Chapter 2). This is the first study in the tropics that provides observational data based on a large sample size of carbon stocks in aboveground and belowground biomass, necromass, and soils. I also report a measure of uncertainty in these estimates and an assessment of the degree spatial variation contributes to the uncertainty of carbon stocks. This study will provide observational data that tropical forest scientists will find useful for testing against theories and models. I believe that

these data will help to reduce the uncertainties of the global carbon budget for the neotropics. In addition, this information provides helpful tools such as biomass equations and methods for managers quantifying carbon stocks and developing CDM projects.

I then present an estimate of the carbon flux in the primary forests of the Porce region (Chapter 3). The purpose of this estimation is to test the null hypothesis that mature tropical forests are in carbon balance. The results presented here can have important implications in the understanding of the carbon balance in the tropics. This is also the first study in the tropics reporting a large set of measurements for the assessment of the ecosystem carbon balance.

Finally, in Chapter 4 I present a modeling exercise to assess the degree population- and community-level processes influence the carbon budget of a hypothetical tropical forest. This tests whether population and community processes may cause a C balance to change in ways that traditional ecosystem models do not predict.

CHAPTER 2

TOTAL CARBON STOCKS IN PRIMARY AND SECONDARY TROPICAL FORESTS OF THE PORCE REGION, COLOMBIA

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Abstract

Detailed ground-based quantifications of carbon stocks in tropical forests are few despite their importance in global carbon science, policies of global warming, and management for C sequestration. Carbon stocks in live aboveground and belowground biomass, necromass, and soils were measured in a heterogeneous landscape composed of secondary- and primary-forest fragments. A total of 110 permanent plots were used to estimate the size of these carbon pools. Local biomass equations were developed and used to estimate aboveground biomass and coarse root biomass for each plot. Herbaceous vegetation, fine roots, coarse and fine litter, and soil carbon to 4 m depth were measured in subplots. In primary forests, mean total carbon stocks (*TCS*) were estimated as 383.7 ± 43.0 Mg C ha^{-1} (± standard error). Of this amount, soil organic carbon to 4 m depth represented 59%, total aboveground biomass 29%, total belowground biomass 10%, and necromass 2%. In secondary forests, *TCS* was 228.2 ± 11.5 Mg C ha^{-1}, and soil organic carbon to 4 m depth accounted for 84% of this amount. Total aboveground biomass represented only 9%, total belowground biomass 5%, and total necromass 1% of *TCS* in secondary forests. The relatively higher proportion of C stored in belowground biomass in secondary forests compared to primary forests was probably a consequence of previous land use.

Monte Carlo methods were used to assess the uncertainty of the biomass measurements and spatial variation. We found that of the total uncertainty of the estimates of *TCS*, the variation associated with the spatial variation of C pools between plots was higher than measurement errors within plots.

Introduction

Precise estimates of carbon stocks in tropical ecosystems are of high relevance for understanding the global C cycle, the formulation and evaluation of global initiatives to reduce global warming, and the management of ecosystems for C sequestration purposes. However, precise knowledge about the absolute and relative distribution of C stocks in tropical forests is very limited (Clark 2004, Houghton 2005).

Estimating carbon stocks and their distribution in different ecosystem pools is important to understand the degree to which C is allocated to labile and stable components. This information is also useful to estimate the amount of C that is potentially emitted to the atmosphere due to land use changes as well as from natural or human-caused fire events. In the tropics, estimates of C stocks using ground-based measurements are usually focused on quantifying the aboveground component (Houghton 2005), while other carbon pools such as belowground biomass, necromass, and soil carbon are generally ignored (e.g., Brown et al. 1995, Kauffman et al. 1998, Clark and Clark 2000, Hughes et al. 2000, Chave et al. 2001, Cummings et al. 2002). Detailed quantifications of total C stocks in tropical areas are scarce, a major cause of uncertainty associated with the assessment of this region's C balance (Schimel et al. 2001, Clark 2004, Houghton 2005).

Although estimations of forest biomass are abundant in the tropics, Houghton et al. (2001) found several problems in published estimates of C stocks from ground-based measurements in Amazonian forests: 1) uncertainty associated with spatial variability, 2) lack of distinction between primary and secondary forests, 3) small inventory areas (< 1

ha), 4) incomplete measurements of all C pools, 5) biased sample designs, 6) inadequate use of regression equations, and 7) lack of continuity in surveys.

The majority of C stocks estimates in neo-tropical forests have been carried out in the Amazon basin with additional estimates from Costa Rica, Mexico, and Panama. Lowland undisturbed tropical forests have received special attention while research in other forest types is lacking despite their large areas, particularly in the case of secondary forests. According to FAO, in 1990 secondary forests accounted for 335 million hectares in Latin America (Smith et al. 1997). In Colombia, secondary forests are an important fraction of total forested area and their distribution is highly heterogeneous, mixed with croplands, grasslands, and primary forests (Etter and van Wyngaarden 2000).

The methodological problems mentioned above, in conjunction with spatial variation of biophysical variables over landscapes, are important sources of uncertainty in the estimation of carbon stocks in forested ecosystems. An average value of C stocks for an ecosystem might not be the best descriptor of this variable when these uncertainties are high. Measures of uncertainty such as the standard error of the mean or the range should be reported in addition to the average, which is the most likely value but not the only possible value.

In this study we present a detailed estimation of C stocks in a tropical premontane landscape composed of a mixture of primary and secondary forests that addresses the methodological issues mentioned above. The first objective of this study was to quantify

the absolute and relative quantities of C stored in different ecosystem pools and the degree of uncertainty in these estimates. The second objective was to compare the relative C stocks between primary and secondary forests for the different carbon pools to assess the effects of land use change.

Methods

Study Site

This study was carried out in the Porce Region, Colombia (6º45'37''N, 75º06'28''W) at the area locally known as Porce II where a dam was constructed in 2000 for hydropower generation (Figure 2.1). Mean annual precipitation between 1990 and 2003 was 1927 ± 272 mm (± standard deviation). Mean annual temperature at 975 m a.s.l. is 22.7ºC, with a monthly minimum of 21.3ºC and a maximum of 24.1ºC. Altitude ranges from 900 to 1500 m, a zone that represents the transition from lowland to premontane moist tropical forests. Soils are derived from granitic rocks, have low fertility, and high acidity. Twenty soil series have been described in the site and grouped in two main orders: Entisol and Inceptisol. The most common soil subgroups are *Ustoxic Dystropept*, *Typic Tropaquent*, and *Typic Tropopsamment* (Jaramillo 1989). Mean bulk density at 30 cm depth in primary forests was estimated as 1.1 Mg m^{-3} and in secondary forests as 1.3 Mg m^{-3}.

Evidence of human settlement dates from 9000 yr B.P. and suggests that shifting cultivation began 2000 yr B.P. (Castillo 1998). After Hispanic colonization (~16th

century), land use changed to intensive cattle ranching, mining, and agriculture in small parcels. During the 1990's, the farms were sold and the land was abandoned due to the dam project, which promoted forest succession. Today, there is a mosaic of primary and successional forests of different ages (approximately between 5 to 25 yr). Primary forest fragments covers nearly 694 ha and secondary forests 1462 ha. Species composition and diversity indexes of these forests were found to be very similar to other primary forests in lowland areas. The main tree species in primary forests, according to their importance value index, are: *Anacardium excelsum*, *Jacaranda copaia, Pouruma cecropiifolia, Virola sebifera, Oenocarpus bataua, Miconia albicans, Vochysia ferruginea, Cordia bicolor, Pera arborea,* and *Pseudolmedia laevigata* (Jaramillo and Yepes 2004). Secondary forests and fallows are dominated by light-demanding tree species such as *Vismia baccifera, Piper aduncum, Myrsine guianensis Jacaranda copaia, Psidium guajaba, Miconia affinis, Erytroxylon sp.* and *Vismia ferruginea* (Jaramillo and Yepes 2004).

Permanent plots

In 1999, 33 permanent plots (20 m x 50 m, 0.1 ha) were established in primary forests and 77 in secondary forests (20 m x 25 m, 0.05 ha) by random assignment on a map for a total sampling area of 7.15 ha. Sampling points were located in the field using a GPS unit. All trees, lianas and palms ≥ 10 cm in *D* (diameter at 1.3 m for trees without irregularities) in primary-forest plots and all plants ≥ 5 cm in secondary-forest plots were measured. Moreover, plants ≥ 1 cm in *D* were measured in subplots (10 m x 10 m in primary forests and 5 m x 5 m in secondary forests) within each plot. Diameters were

measured using conventional calipers for plants ≥ 10 cm and digital calipers for plants 10 > *D* ≥ 1 cm. For buttressed trees, *D* was measured just above the highest buttress. Trees with irregularities were measured following the protocols reported by MacDicken (1997).

In each plot, six 1 m^2 subplots were established to harvest all herbaceous and non-woody vegetation < 1 cm in *D* and all standing litter. Coarse woody debris (> 2 cm in diameter) was measured in 25 m^2 subplots. The material was weighed *in situ* and representative samples were collected to estimate dry weights in the laboratory of Ecology and Environmental Conservation, National University of Colombia at Medellín. Fine root biomass was sampled using soil cores (7 cm diameter, 15 cm long) down to 30 cm depth. Only 3 plots were sampled in primary forests and 10 in secondary forests due to the laborious nature of the work. A detailed description of the methods used to sample fine roots is described in Sierra et al. (2003). In all plots, 20 soil samples were taken to 30 cm depth. These 20 samples were mixed together and a sub-sample was taken and used to estimate C content with the Walkley-Black method (Walkley and Black 1934). Four soil cores per plot in all plots were used to estimate soil bulk density. Additionally, six plots in each forest type were randomly selected to measure soil C to 4 m depth. Soil pits of 80 cm x 120 cm x 430 cm were excavated and four soil samples per pit were taken at 5, 10, 20, 30, 50, 75, 100, 150, 200, 250, 350, and 400 cm depth. Two of these samples were used for soil C content determination and the other two for bulk density estimation. Soil C content was estimated using the dry combustion method in a C-N analyzer (Carlo Erba NC 1500).

Biomass equations

Trees, palms and lianas were harvested and measured to collect data for local biomass equations. Individuals were selected over their entire size range to avoid extrapolations in predicting biomass of large trees.

A total of 292 trees were harvested and measured in primary and secondary forests (range in *D* was 0.3 – 198.9 cm). Diameter and height (*H*) were measured on every tree. Total weight of foliage, branch and bole was estimated for every tree by measuring total fresh weight in the field and drying representative samples in the laboratory to determine moisture content. Biomass equations were fit for each forest type (primary and secondary), using *D* or *H* as independent variables.

The root system of 69 trees was excavated to estimate coarse root (≥ 5 mm) biomass. The range of sampled trees was 1.7 - 64.6 cm in *D*. An allometric equation was developed with these data using *D* as the independent variable.

To estimate palm biomass, 41 individuals were sampled and used to fit aboveground biomass equations. A biomass equation for the species *Oenocarpus bataua* was developed separately from other palm species because of its distinct growth pattern and allometry (Hallé et al. 1978). Carbon content in biomass was estimated using 82 samples from different pools and processed with a C-N analyzer.

Calculations

Total basal area was calculated for every plot in units of m^2 ha^{-1} summing up the basal area of each tree at 1.3 m height and extrapolating to a hectare. Mean basal area was calculated for each forest age-class averaging the estimates from each set of plots (primary and secondary).

TCS was estimated by aggregating the mean amount of carbon in different pools (total aboveground biomass (*TAGB*), total necromass (*TN*), total belowground biomass (*TBB*), and soil organic carbon (*SOC*), Figure 2.2):

$$\hat{\mu} = \hat{\mu}_{TAGB} + \hat{\mu}_{TN} + \hat{\mu}_{TBB} + \hat{\mu}_{SOC} \quad (1)$$

TAGB was obtained as the sum of the amount of carbon in the aboveground carbon pools (above ground biomass of trees > 1 cm in *D* (*ABT*), aboveground biomass of *O. bataua* (*ABOB*), aboveground biomass of other palms (*ABOP*), aboveground biomass of lianas (*ABL*), and aboveground biomass in herbaceous and non-woody vegetation (*AHNWV*)):

$$\hat{\mu}_{TAGB} = \left(\hat{\mu}_{ABT} + \hat{\mu}_{ABOB} + \hat{\mu}_{ABOP} + \hat{\mu}_{ABL} + \hat{\mu}_{AHNWV}\right) * C\,, \quad (2)$$

where *C* is the conversion factor from biomass to carbon. With the exception of *AHNWV*, all carbon pools in equation (2) were estimated in each sampling plot by measuring the diameter *D* (cm) or the height *H* (m) of each individual and then applying a biomass equation (results in kg).

The second term of equation (1), mean total necromass ($\hat{\mu}_{TN}$), was calculated as the aggregation of fine litter (*FL*), coarse woody debris (*CWD*) and snags (*SNG*):

$$\hat{\mu}_{TN} = \left(\hat{\mu}_{FL} + \hat{\mu}_{CWD} + \hat{\mu}_{SNG}\right) * C \,. \tag{3}$$

The third term of equation (1), carbon in total belowground biomass ($\hat{\mu}_{TBB}$), is composed of the biomass of fine (*FR*) and coarse roots (*CRB*):

$$\hat{\mu}_{TBB} = \left(\hat{\mu}_{CRB} + \hat{\mu}_{FR}\right) * C \tag{4}$$

The estimation of the last term in equation (1), soil organic carbon ($\hat{\mu}_{SOC}$), was obtained by combining the data of bulk density and %carbon content in soil (Rosenzweig and Hillel 2000). A regression model that predicts soil organic carbon at depth was developed. Using mathematical integration of the regression equation, an estimate of soil carbon to 4 m depth was computed. A detailed description of the methods to estimate soil carbon is reported by Moreno (2004).

Statistical analysis

Biomass equations were fit to the data using linear and non-linear regression techniques. To avoid systematic bias in the utilization of the back-transformed logarithmic equations, a correction factor was used (Heien 1968). The correction factor applied equals half the mean square error from the regression (MSE/2) and was added to the independent term of

the equation. An index proposed by Overman et al. (1994) was used for model checking and comparison, with a slight modification to identify over- or under-estimation:

$$\delta B = \frac{\sum_{i=1}^{n} \frac{\left(\hat{Y}_i - Y_i\right)*100}{Y_i}}{n}, \quad (5)$$

where $\hat{Y}_i$ is the estimated tree mass, Y_i is the measured mass of the *i*th tree and *n* is the total number of trees used to test the equation.

A Monte Carlo analysis was performed to calculate the uncertainty around the final estimate of mean total carbon stocks (*TCS*). Total uncertainty was estimated in two separate components: the uncertainty of each pool within plots due to measurement errors (S_{within}) and the spatial variation among plots ($S_{between}$). S_{within} was calculated as the averaged variation between sub-plots within plots. For pools that were estimated using biomass equations, S_{within} was calculated as: $\hat{\sigma}_A = B\sqrt{\exp(MSE) - 1}$, with *B* as the estimate of the average biomass for any pool, and *MSE* the mean square error from the biomass equation. The spatial variation ($S_{between}$) was calculated as the standard error of the mean biomass among plots. Total uncertainty (S_{total}) was estimated as the sum of the within and between uncertainty for every pool ($S^2_{total} = S^2_{within} + S^2_{between}$).

Using the estimated uncertainty of each carbon pool and assuming normal distributions, a Monte Carlo procedure was used to estimate the uncertainty of the final estimates of *TAGB*, *TN*, *TBB*, and *TCS*. Random numbers were sampled from the distribution of each

C pool and then summed up to produce an estimate of the aggregated pool. The procedure was repeated 10,000 times. The standard deviation of the distribution of the averages (i.e., the standard error of the mean) was used as an estimate of the uncertainty of each aggregated pool. Upper and lower 95% confidence limits for the average of aggregated pools and *TCS* were calculated by multiplying these standard deviations by 1.96 (t-value at $p = 0.975$ for ∞ degrees of freedom). Monte Carlo simulations were run in R 1.8.0 for Windows (Ihaka and Gentleman 1996).

Results

Basal area

Mean basal area in primary forests was 36.85 ± 10.93 m^2 ha^{-1} (± standard deviation), and 12.92 ± 7.71 m^2 ha^{-1} in secondary forests. Mean basal area was significantly different between both forest types (p-value < 0.0001, from a two sample t-test). For both forest types a high degree of spatial variation was observed (Figure 2.3). Three plots showed a high basal area in primary forests. These plots were established (as the result of randomness) in sites in which large trees of the species *Anacardium excelsum* were clustered.

Biomass equations

Tree diameter satisfactorily explained the variation in individual tree biomass for aboveground and belowground pools with the exception of palms, for which height was the best explanatory variable (Table 2.1). All measured trees were in the range of *D* or *H* sampled for the aboveground biomass equations. Coarse root biomass was extrapolated

for 23 trees (out of 11,323) that fell outside the range of tree sizes sampled to fit the equations.

Uncertainty analysis

Aboveground biomass of trees was the largest biomass pool and had the highest uncertainty, for both primary and secondary forests (Table 2.2). The high uncertainty is mainly explained by the variation of *ABT* estimates between plots. In general, this pattern ($S_{within} < S_{between}$) was found for the majority of the biomass pools, suggesting that the spatial variation of biomass among plots tends to be higher than the uncertainty in measuring each pool within each plot. In general, the uncertainty range for primary forests was higher than the uncertainty range in secondary forests. In primary forests the uncertainty of *TCS* in relative terms was 11% while in secondary forests this uncertainty was only 5%.

Biomass estimations

In primary forests, total aboveground biomass was estimated as 247.8 ± 38.2 Mg ha^{-1} and in secondary forests this estimate was 46.4 ± 3.9 Mg ha^{-1} (Table 2.3). The main fraction of aboveground biomass (92-95%) was composed by trees > 1 cm in *D* in both forest age-classes. Palm biomass represented a minor fraction (6%) of total aboveground biomass in primary forests and was a very small fraction (0.6%) in secondary forests as well; however palm biomass in primary forests was considerable higher (Table 2.3). Estimated *TAGB* in primary forests was about 5 times greater than in secondary forests. From the total mass (*TM*) of both forest types, which is composed by the sum of aboveground

biomass, belowground biomass, and aboveground necromass, *TAGB* represented 71.6% and 58.6% in primary and secondary forests, respectively (Table 2.4). Total mass in primary forests was estimated as 346.2 ± 41.8 Mg ha^{-1} and 79.2 ± 4.8 Mg ha^{-1} in secondary forests, and thus it was about four-fold larger than the former.

Total belowground biomass (*TBB*) was higher in primary forests than in secondary forests (Table 2.4). In primary forests *TBB* was estimated as 83.7 ± 16.8 Mg ha^{-1}, dominated by coarse root biomass (80% of this amount). In contrast, secondary forest *TBB* was estimated as 25.5 ± 2.5 Mg ha^{-1}, with fine roots representing an important fraction of this pool (60.8%). *TBB* represented 24.2% and 32.2% of *TM* in primary and secondary forests, respectively.

Total aboveground necromass (*TN*) was 14.7 ± 2.6 Mg ha^{-1} in primary forests and 7.3 ± 0.6 Mg ha^{-1} in secondary forests. Although *TN* was higher in primary forests it represented a higher fraction of total mass in secondary forests (9.2%) than in primary forests (4.2%). Most of the necromass in secondary forests is composed of fine litter (67%).

Soil Organic Carbon (SOC)

Organic C concentrations in soils in the first 30 cm were estimated as 29.8 ± 0.73 mg g^{-1} for primary forests and 23.4 ± 0.6 mg g^{-1} for secondary forests. Evidence for a reduction of organic carbon concentrations in secondary forests was observed (p-value < 0.05 from a two-sample comparison) compared to primary forests. Using a correction factor for the

differences in bulk density between forest age-classes, the estimated *SOC* to 30 cm depth was 96.60 ± 2.47 Mg ha^{-1} in primary forests and 72.18 ± 2.54 Mg ha^{-1} in secondary forests (Table 2.5).

Estimated *SOC* to 4 m depth was 227.9 ± 38.3 Mg ha^{-1} in primary forests and 192.5 ± 11.1 Mg ha^{-1} in secondary forests (Table 2.5). Estimated *SOC* to 30 cm represented 42% of the *SOC* to 4 m in primary forests and 37% in secondary forests.

Total C stocks

Mean C content in biomass (*C*) was 0.45 ± 0.01. This value was used to estimate C densities in above- and below-ground biomass and necromass. In primary forests mean *TCS* was 383.7 ± 43.0 Mg C ha^{-1} and was mainly composed by *SOC* (59%). In secondary forests, mean *TCS* was 228.2 ± 11.5 Mg C ha^{-1} and *SOC* represented 84% of this amount (Table 2.5).

Ratios between carbon pools were calculated (Table 2.6). These ratios represent C fractions between pools and can be used to estimate the proportion of C stored in different ecosystem pools (e.g. the *TBB*:*TAGB* ratio is analogous to the widely know root:shoot ratio at an ecosystem scale). In primary forests C stored in *TAGB* was 29% of *TCS*, while in secondary forests it was only 9%. Carbon in *TBB* was equivalent to 55% of the C in *TAGB* in secondary forests and 34% in primary forests. However, C in *TBB* was only 10% of *TCS* in primary forests and 5% in secondary forests. Carbon in total live biomass (*TLB* = *TAGB* + *TBB*) was a higher percentage of *TCS* in primary forests (39%)

than in secondary forests (14%). Carbon in *TN* was 6% and 16% of the C in *TAGB* for primary and secondary forests, respectively; but its contribution to *TCS* is negligible (between 1 and 2% in both forest types).

Discussion

Biomass equations

The local equation of aboveground biomass for primary forest was compared with other biomass equations estimated in other tropical forests (Crow 1980, Overman et al. 1994, Brown 1997, Chave et al. 2001). We found that the equation for wet forests proposed by Brown (1997) overestimated aboveground biomass by almost 60% (Table 2.7). The equation proposed by Chave et al. (2001) estimated aboveground biomass for the sampled trees with a slight overestimation (9%). For secondary forest trees, Brown's (1997) equation for wet forests overestimated aboveground biomass by as much as 70% in large trees, but only 3% in small trees. This comparison highlights the importance of using local information to develop biomass equations. Using biomass equations developed in different locations increases the uncertainty of biomass estimates. This issue is rarely addressed in the literature, although use of off-site biomass equations is a common practice.

In both primary and secondary forests, our estimate of *TBB* was higher than the predicted using the root biomass equations developed by Cairns et al. (1997) (45.4 and 10.3 Mg ha^{-1}, for primary and secondary forests respectively). Our estimate of average *TBB* is even higher than the upper confidence limit estimated with Cairns et al.'s (1997) equation

for tropical regions. Although these authors point out that their equation is more appropriate to derive regional estimates, it has been proposed to estimate belowground biomass at the stand level (see Brown 2002). Our results show that large underestimation of *TBB* can occur by using indirect methods to estimate belowground C pools. However, it is important to note that our estimate of *FR* is in the upper range of estimates reported for the tropics. A procedure to account for root losses in the washing and sorting process was used in this study (Sierra et al. 2003) which increased fine root biomass average 50% above the non-corrected estimate. However, even if this correction factor was not used total belowground biomass would still be higher than the estimates using Cairns et al.'s (1997) equation.

Plot size and spatial variability

Typically, C-stock studies are conducted within a single forest type to reduce the variation associated with spatial heterogeneity. Large sampling plots (> 0.25 ha as proposed by Clark and Clark 2000) are used to minimize the variation within the forest type. The notion of homogeneous space (Turner and Chapin 2005) is implicit in those studies. Using a modeling exercise, Smithwick et al. (2003) have shown that the homogeneous approach in the study of C dynamics for a heterogeneous landscape could lead to erroneous representations of broad-scale processes. To capture these small-scale processes a large sample size is helpful. A large number of sampling plots is also useful to assess the spatial variation of C stores when the landscape is a mosaic of forests with different ages, disturbance regimes, and legacies.

In terms of C stocks the study site is a spatially complex landscape because it comprises a large number of patches of different land use history, soil, slope, and donor ecosystems for regenerating secondary forests. The interaction of these factors produces a high variation in forest cover within the landscape (Figure 2.3).

In this study we preferred to establish a large number of small plots instead of the classical establishment of a large single sampling unit due to the landscape complexities mentioned above. A large number of plots allows the estimation of spatial variability of carbon stocks, which increases the confidence in the C estimates (i.e. a large number of samples reduces the standard error of the mean). The coefficient of variation of the estimates of aboveground tree biomass shows that at least 20 plots of 0.1 ha are required to obtain a standard error of the mean less than 20% relative to the average (Figure 2.4). This result contrasts with those of Nascimento & Laurance (2001) who found that three plots of 1 ha can provide a precise estimate of aboveground biomass. This contradiction may be explained by the fact that Amazon forests tend to be fairly homogenous over the landscape whereas premontane forests in the Andes are patchy and heterogeneous (Etter and van Wyngaarden 2000, Armenteras et al. 2003). With three samples it would not be possible to sample the actual level of variation over the latter landscape.

Importance of including an uncertainty analysis

The inclusion of uncertainty analyses is not common in the literature related to estimates of C pools in forest ecosystems (however see Ketterings et al. 2001, Chave et al. 2004, Harmon et al. 2004). This type of analysis helps to identify the major drivers of variation

of C pools in forest ecosystems. Our analysis showed that the error associated with measuring C pools in these forests was usually lower than the variation of the pools themselves across the landscape. This study also shows that a large number of sampling plots reduces the uncertainty in the final estimates. Further study designs for carbon inventories in heterogeneous landscapes should focus on obtaining more replicates of the sampling unit rather than the extent of the unit itself. Here we found that the variation of the larger pools such as soil carbon is the main source of the variation in the final estimate of aggregated pools. This indicates that more effort should be directed in the sampling intensity and accuracy of large pools.

Soil carbon was the largest C pool in the ecosystems studied; however, our estimate has high uncertainty, mainly due to the size of this pool and the small number of samples used to estimate *SOC* to 4 m depth (6 plots per forest type). Because of this uncertainty, significant differences were not found in *SOC* to 4 m depth between primary and secondary forests (p-value = 0.156, from a t-test).

Total carbon stocks in primary forests are more variable than in secondary forests. In primary forests a 95% confidence interval for mean *TCS* was estimated as 299.4 to 467.9 Mg C ha^{-1}, while for secondary forests this interval is only 206.0 to 250.4 Mg C ha^{-1}. Although most of this variation is explained by the uncertainty in the estimation of *SOC*, it is interesting that the variation of the estimates of *ABT* are very similar between primary and secondary forests (Figure 2.4). In secondary forests a number of factors may be associated with this variation, previous land use and age being the most important.

Similarly, natural disturbances in primary forests seem to play an equivalent role in terms of the variation of C stocks.

Comparison to other regions

Although the primary forests studied here are located in the premontane moist life zone (*sensu* Holdridge), our estimation of aboveground biomass is in the range of other estimates in moist and wet lowland tropical forests. The confidence interval obtained here for the average *TAGB* in primary forests (207.3, 322.7 Mg ha^{-1}) is consistent with other estimates of *TAGB* in tropical sites. The estimated mean *TAGB* for primary forests in this study is similar to those found in old-growth lowland moist forests in Barro Colorado Island, Panama (214.4 ± 46.4 Mg ha^{-1}) and La Selva, Costa Rica (234.0 ± 60.9 Mg ha^{-1}) (DeWalt and Chave 2004), although these estimates are biased to locations of tall forests without gaps. Laurance et al. (1997) found that biomass tends to decline in forest edges as an effect of fragmentation. The primary forest fragments in our study area indicate that even after the dramatic effects of fragmentation these forest remnants can still store large amounts of carbon. Our estimate is also in the range of estimates of aboveground live biomass for the Amazon (Houghton et al. 2001). These results suggest that changes in altitude, at least up to 1500 m a.s.l., do not play an important role in determining *TAGB* in tropical forests. Instead, precipitation and anthropogenic interventions may be more important factors explaining stores of *TAGB*.

Relative importance and stability of pools

In our area, lianas play a more important role in secondary than in primary forests. Conversely, palms are more prominent in primary forests (Table 2.3). This pattern reflects a change in forest composition, probably due to changes in light availability as succession proceeds to older stages. However, this change in community structure is not associated with important changes in the relative distribution of aboveground biomass. Trees > 1 cm in diameter represent more than 90% of *TAGB* in both forest types, which highlights the relevance of quantifying this C pool in tropical forest ecosystems.

TAGB is the most sensitive of all pools to anthropogenic interventions. In primary forests *TAGB* is five times higher than in secondary forests, while *TBB* and *TN* are only three and two times higher, respectively.

Although the difference of *SOC* to 4 m depth between the two forest types was not significant, the net difference between the two forest types was 35.4 Mg ha^{-1}. At 30 cm depth, where the sample size was higher and land use changes are more pronounced, the difference between the two forest types was significant (p-value < 0.05 from a t-test). For the other C pools (*TAGB*, *TBB*, and *TN*) differences between primary and secondary forests are enormous due to the anthropogenic disturbances. These data show that soils are more resistant than any other pool to C losses associated with human perturbations.

Following deforestation these forests were used for cattle pastures and as a result some soil properties such as structure were degraded. This disturbance is probably also

associated with the observed increase in the *TBB*:*TAGB* ratio from primary to secondary forests. Here we hypothesize that different resource limitations between the two forest age-classes are responsible for a shift in C allocation from aboveground to belowground plant parts when primary forests are converted to secondary forests. The high contribution of fine root biomass to *TM* in secondary forests suggests that belowground limitations are higher in this forest type than in primary forests (Chapin et al. 2002). Increased light competition as succession advances probably plays a more important role in the allocation of C to aboveground plant parts in primary forests.

Effects of land use

For the entire area of study (2156.5 ha) the 95% confidence interval of carbon stored in the ecosystems is between 509.1 and 690.8 Gg with a mean of 601.0 ± 34.0 Gg C. If these forests were not deforested previously they would store between 650.0 and 1009.9 Gg C, which is on average 38% more carbon than what is currently stored in the area.

Given our results, the deforestation of one hectare of primary forests in the Porce region would cause the emission of about 155.8 ± 19.0 Mg C to the atmosphere. The deforestation of all the remaining primary forests of this region would cause the emission of 108.4 ± 13.1 Gg C. We estimate that the amount of carbon emitted to the atmosphere in this region at the time of forest to pasture or agriculture conversion was between 174.0 and 283.2 Gg C.

Since secondary forests cover a larger area (67.8% of the total area) than primary forests (32.2%), the total amount of carbon stored in secondary forests (333.7 Gg) is higher than in primary forests (266.2 Gg). However, in terms of the relative contribution of each forest type to *TCS* in the landscape, primary forests contained nearly the same proportion as secondary forests (44.4% and 55.6%, respectively). This means that about a half of the carbon in the landscape is stored on a third of the land.

Assuming that primary forests are in a C balance we believe that the total area is acting as a carbon sink because secondary forest is the dominant forest type in this landscape. These regrowing forests are recovering from previous disturbances and eventually should reach an average biomass close to the biomass in the primary forests. However, if the decline in forest edges as an effect of fragmentation similarly to the degree Laurance et al. (1997) found, then it is possible the primary forest remnants are a source and the overall landscape is less of sink than indicated from the secondary forests alone. This hypothesis only could be tested by monitoring changes in C stocks and fluxes over time.

Homogenous areas of tropical forests are decreasing with secondary and primary forest fragments playing an increasing role in the composition of tropical landscapes. This study shows that heterogeneous landscapes can store important quantities of carbon but impose additional challenges for their study such as sampling intensity. Efforts to study the global C balance, especially in the tropics, should acknowledge the increasing role of heterogeneous landscapes due to anthropogenic perturbations and natural variability. A

landscape approach to studying the C balance and the biogeochemistry of tropical forests would improve our ability to address global questions about elemental cycles.

Tables

Table 2.1. Biomass equations used in the estimation of different C pools (n = number of individuals used to fit the equation, *CF*: correction factor for the allometric models, R^2: coefficient of determination.

Carbon pool	*Equation*	Range in D or H (cm)	n	*CF*	R^2 (%)
Aboveground tree biomass in primary forests ($D \geq 1$ cm)	ln (*ABT*)= -2.286 + 2.471 ln (*D*)	0.5-198	140	0.091	97.90
Aboveground tree biomass in secondary forests ($D \geq 1$ cm)	ln (*ABT*) = -2.232 + 2.422 ln (*D*)	0.9-40	152	0.083	97.47
Coarse root biomass (primary and secondary forest)	ln (*CRB*) = - 4.394 + 2.693 ln (*D*)	1.0-64.6	49	0.316	91.79
Aboveground biomass for *Oenocarpus bataua*	$ABOB = 139.48 + 7.308\ H^{1.133}$	50-250	83	*	82.95
Aboveground biomass for other palms	ln (*ABOP*) = 0.360 + 1.218 ln (*H*)	100-150	37	0.325	65.28
Aboveground biomass for lianas	ln (*ABL*) = 0.028 + 1.841 ln (*D*)	1-11	33	0.133	87.44

Table 2.2. Estimates of uncertainty for each pool. Total variation (S_{total}) was partitioned between within (S_{within}) and between ($S_{between}$) variation. *n*: number of sampling units, SE: standard error of the mean, and $\hat{\mu}$: estimate of mean biomass for each pool. Units in Mg ha^{-1}.

Pool	S_{within}	$S_{between}$	S_{total}	*n*	*SE*	$\hat{\mu}$
Primary forests						
ABT	104.19	190.50	217.13	33	37.80	228.90
ABOB	3.12	14.93	15.25	33	2.66	8.93
AOPB	5.57	7.90	9.67	33	1.68	5.82
ABL	1.95	3.29	3.82	33	0.67	3.48
AHVNW	0.74	0.22	0.78	33	0.14	0.65
FL	2.44	0.78	2.56	33	0.45	6.03
CWD[a]	NA	NA	7.25	33	1.26	6.07
SNG	3.23	4.01	5.15	33	0.90	2.67
CRB	63.89	68.93	93.99	33	16.36	67.07
FR	3.45	2.89	4.50	3	2.60	17.38
Secondary forests						
ABT	18.76	29.00	34.54	77	3.94	43.91
AOPB	0.32	2.85	2.87	77	0.33	0.33
ABL	0.74	2.22	2.34	77	0.27	1.33
AHVNW	1.05	0.41	1.13	75	0.13	0.92
FL	2.03	1.91	2.79	75	0.32	4.88
CWD[a]	NA	NA	4.21	77	0.48	2.02
SNG	0.49	0.93	1.06	77	0.12	0.41
CRB	9.36	7.22	11.82	77	1.35	9.94
FR	4.55	4.78	6.60	10	2.09	15.54

[a] Variation cannot be partitioned because there were not replications within plots.

Table 2.3. Estimates of aboveground biomass for different pools in primary and secondary forests.

	Primary forests		*Secondary forests*	
	Mean biomass (Mg ha^{-1}) ± *SD*	Percentage of *TAGB*	Mean biomass (Mg ha^{-1}) ± *SD*	Percentage of *TAGB*
Trees > 1 cm	228.9 ± 37.8	92.4	43.9 ± 3.94	94.6
Palms (*Oenocarpus bataua*)	8.9 ± 2.7	3.6	0	0
Other palms	5.8 ± 1.7	2.3	0.3 ± 0.3	0.6
Lianas	3.5 ± 0.7	1.4	1.3 ± 0.3	2.8
Herbaceous vegetation	0.6 ± 0.1	0.3	0.9 ± 0.1	1.9
Total Aboveground Biomass (*TAGB*)	247.8 ± 38.2	100	46.4 ± 3.9	100

Table 2.4. Estimates of total aboveground biomass (TAGB), total necromass (TN), total belowground biomass (TBB) and total mass (TM) for primary and secondary forests.

	Primary forests		*Secondary forests*	
	Mean Mass ± *SD* (Mg ha^{-1})	Percentage of Total Mass	Mean Mass ± *SD* (Mg ha^{-1})	Percentage of Total Mass
TAGB	247.8 ± 38.2	71.6	46.4 ± 3.9	58.6
Fine litter	6.0 ± 0.4	1.7	4.9 ± 0.3	6.2
CWD	6.1 ± 1.3	1.8	2.0 ± 0.5	2.5
Snags	2.7 ± 0.9	0.8	0.4 ± 0.1	0.5
TN	14.7 ± 1.6	4.2	7.3 ± 0.6	9.2
Coarse roots	67.1 ± 16.4	19.4	9.9 ± 1.3	12.5
Fine roots	17.4 ± 2.6	4.8	15.5 ± 2.1	19.6
TBB	83.7 ± 16.8	24.2	25.5± 2.5	32.2
TM	346.2 ± 41.8	100	79.2 ± 4.8	100

Table 2.5. Estimates of C in total aboveground biomass (*TAGB*), total necromass (*TN*), total belowground biomass (*TBB*), soil (*SOC*) at 0.3 and 4 m depth, and total C stocks (*TCS*) in primary and secondary forests.

	Primary forests		*Secondary forests*	
	C Stock (Mg C ha^{-1})	% of *TCS*	C Stock (Mg C ha^{-1})	% of *TCS*
TAGB	111.6 ± 17.3	29.1	20.9 ± 1.8	9.1
TN	6.6 ± 0.7	1.7	3.3 ± 0.3	1.4
TBB	37.6 ± 7.6	9.8	11.5 ± 1.1	5.0
SOC (0-30 cm)	96.6 ± 2.5	25.2	72.2 ± 2.5	31.6
SOC (0-4 m)	227.9 ± 38.3	59.4	192.5 ± 11.1	84.4
TCS	383.7 ± 43.0	100	228.2 ± 11.5	100

Table 2.6. Ecosystem C pool ratios in primary and secondary forests.

		TAGB	*TN*	*TBB*	*TLB*	*SOC*	*TCS*
	Primary forests			*Numerator*			
Denominator	*TAGB*	1.00	0.06	0.34	1.34	2.04	3.44
	TN	16.83	1.00	5.66	22.49	34.38	57.87
	TBB	2.97	0.18	1.00	3.97	6.07	10.22
	TLB	0.75	0.04	0.25	1.00	1.53	2.57
	SOC	0.49	0.03	0.16	0.65	1.00	1.68
	TCS	0.29	0.02	0.10	0.39	0.59	1.00
	Secondary forests						
	TAGB	1.00	0.16	0.55	1.55	9.21	10.92
	TN	6.33	1.00	3.48	9.82	58.33	69.15
	TBB	1.82	0.29	1.00	2.82	16.74	19.84
	TLB	0.65	0.10	0.35	1.00	5.94	7.04
	SOC	0.11	0.02	0.06	0.17	1.00	1.19
	TCS	0.09	0.01	0.05	0.14	0.84	1.00

Table 2.7. Comparison of aboveground biomass estimates for trees > 1 cm using different biomass equations.

Biomass equation	**Range in *D* (cm)**	***δB***	**Source**
$ABT = 0.102\ D^{2.471}$	0.5-200	12.92	This study
$ABT = 0.118\ D^{2.53}$	5-148	57.64	Brown (1997)
$ABT = 0.118\ D^{2.41}$	> 10	8.78	Chave et al. (2001)
$ABT = 0.139\ D^{2.248}$	Not reported	-19.58	Overman et al. (1990)
$ABT = 0.064\ D^{2.634}$	> 4	18.26	Crow (1980)

Figures

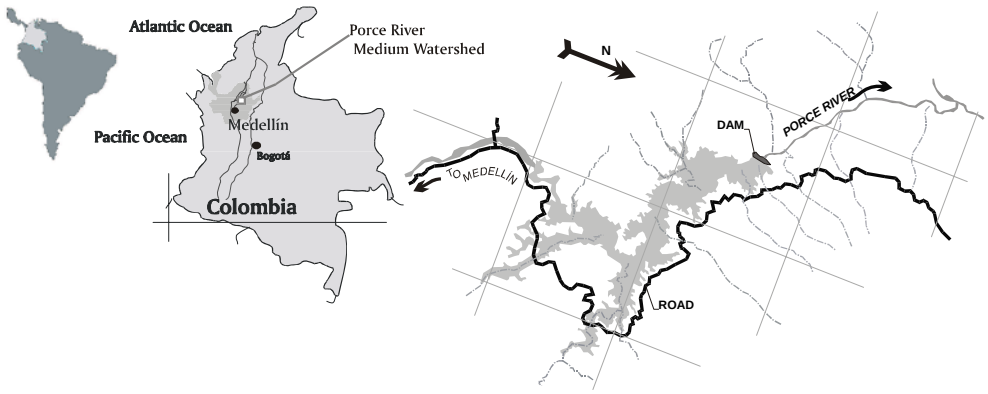

Figure 2.1. Location of the study site. Permanent plots were located surrounding the reservoir (grey area of the map in the right side.

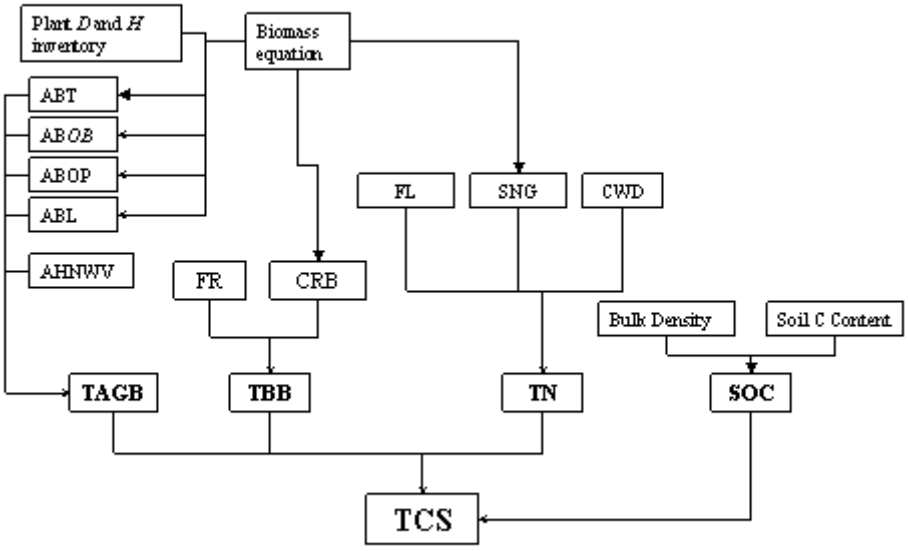

Figure 2.2. Carbon pools assessed in this study. *D*: diameter at breast height, *H*: plant height, *ABT*: Above ground biomass of trees > 1 cm in *D*, *ABOB*: Aboveground biomass of *O. bataua*, *ABOP*: Aboveground biomass of other palms, *ABL*: Aboveground liana biomass, *AHNWV*: aboveground biomass of herbaceous and non-woody vegetation, *TAGB*: Total aboveground biomass, *CRB*: Coarse root biomass, *FR*: Fine root biomass, *TBB*: Total belowground biomass, *FN*: fine litter, *SNG*: snags, *CWD*: Coarse woody debris, *TN*: Total necromass, *SOC*: soil organic carbon, and *TCS*: Total carbon stocks.

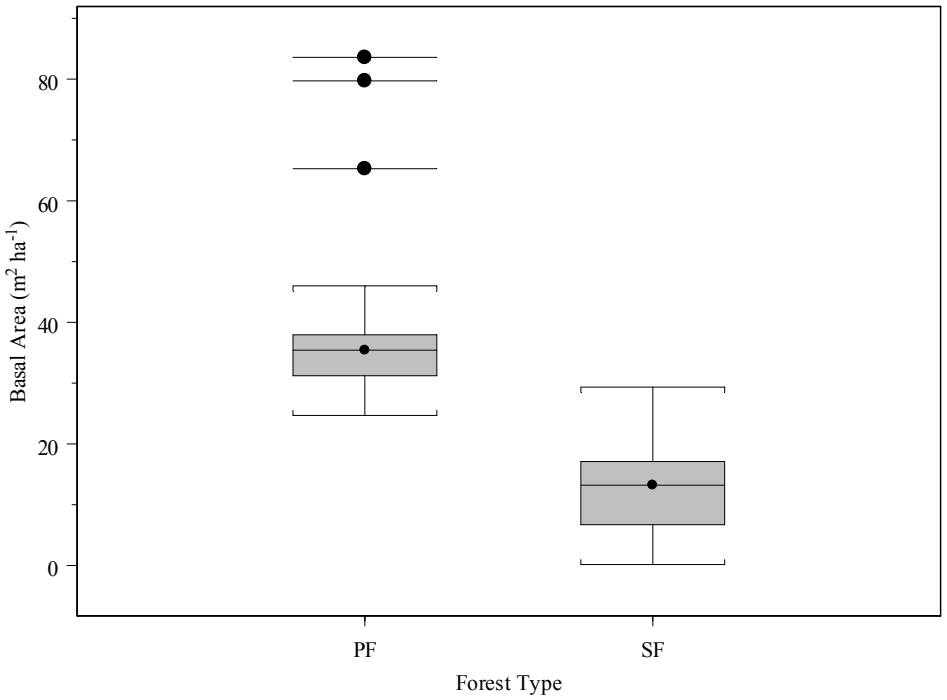

Figure 2.3. Box and whisker plot of basal area in primary and secondary forests.

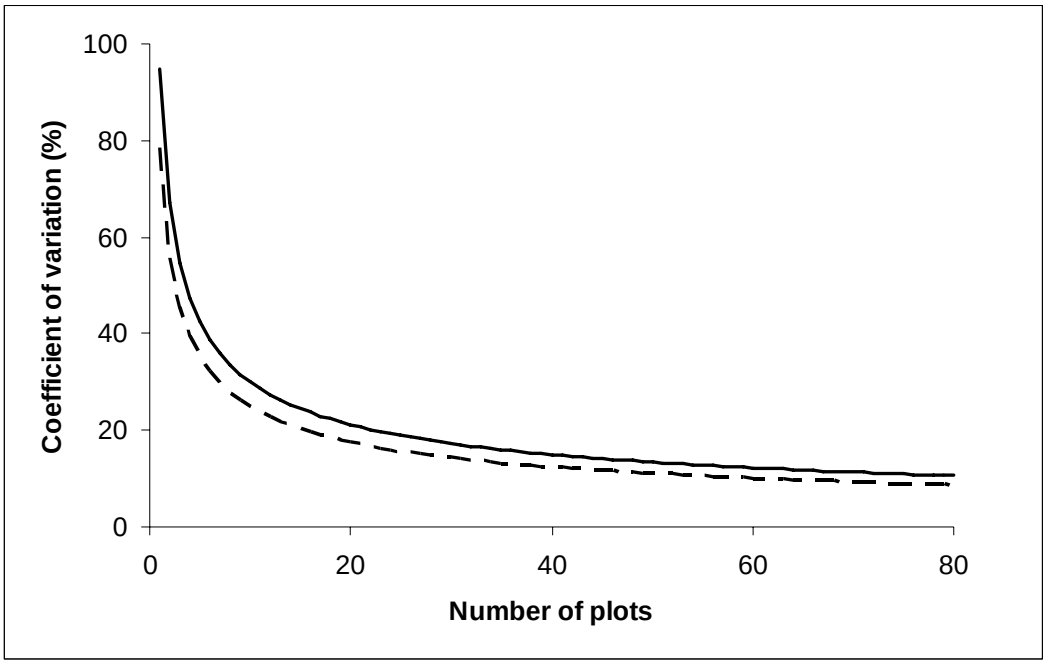

Figure 2.4. Effect of increasing number of plots on the variation in the estimate of mean *ABT* in primary (continuous line, 0.1 ha plots) and secondary forests (discontinuous line, 0.05 ha plots).

CHAPTER 3

SPATIAL AND TEMPORAL VARIATION OF NET ECOSYSTEM PRODUCTION IN A PRIMARY TROPICAL FOREST IN THE PORCE REGION, COLOMBIA

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Abstract

Tropical forest ecosystems play an important role in the global carbon balance. Depending on age and land use, they can act as carbon sources, sinks, or be in approximate balance, but it is uncertain if global environmental changes are forcing these ecosystems outside their natural range of variation. We asked the question of whether or not the net carbon flux of primary forests of the Porce region in Colombia, which should be in balance over the long term, is within the expected range of natural variation. A simple Bayesian hypothesis testing method was used to address this question. Net ecosystem production was measured in this forest in a set of 33 permanent plots from 2000 to 2002 in two, one-year intervals. Changes in above and belowground biomass, as well as fine litterfall, were measured during these intervals to estimate net primary production. Heterotrophic respiration was estimated by measuring litter decomposition rates and soil respiration by the trenching method. Our estimate of net ecosystem production ranged between -4.03 and 2.22 Mg C ha^{-1} yr^{-1} for the two intervals. This range was compared to *a priori* defined range of natural variation estimated from the ecosystem model STANDCARB, which estimated spatial and temporal variation due to gap dynamics. The prior range of variation was estimated between -1.5 and 1.5 Mg C ha^{-1} yr^{-1}. The observed data on net ecosystem production did not provide sufficient evidence to reject the null hypothesis posed. We concluded that the ecosystem is likely behaving within its range of natural variation, but measurement uncertainties were a major limitation to finding evidence to reject the null hypothesis.

Introduction

The role of tropical forests as carbon sources or sinks has been a topic highly debated in the last decade (Clark 2004). Some studies have found that mature tropical forests are important carbon sinks that are possibly affected by global change (Grace et al. 1995, Malhi et al. 1998, Phillips et al. 1998). Other studies have found mature tropical forests to be neutral in the net exchange of C with the atmosphere (Loescher et al. 2003, Saleska et al. 2003, Miller et al. 2004, Rice et al. 2004). The latter studies suggest an important role of climatic variations such as El Niño events in determining the direction and magnitude of the C flux. Thus, while the long-term average indicates the C flux is near zero, it can be positive (sink) or negative (source) in any given year.

Measuring C fluxes in tropical forest ecosystems is a difficult task and all the studies reported so far had been constrained by technical difficulties which can limit interpretation of the results. Studies developed using the eddy covariance technique (Baldocchi 2003) have encountered problems in measuring fluxes at night and under still-air conditions (Baldocchi 2003, Clark et al. 2003, Loescher et al. 2003, Martens et al. 2004, Miller et al. 2004). Early studies that used this technique (Fan et al. 1990, Grace et al. 1995, Malhi et al. 1998) directly measured net ecosystem exchange (NEE) during time periods shorter than 1 year. This can bias the observations to either dry or wet seasons giving erroneous interpretation of the annual flux of C. Longer observations (up to 3 years) have shown that NEE has high interannual variation (Loescher et al. 2003, Saleska et al. 2003). Contrary to early studies that suggested an important C sink in the tropics, the latter studies with improved techniques, longer measurement intervals, and

corroboration with independent ground-based data showed that mature tropical forests can be neutral or even sources of C during dry years. However, there are still limitations in interpreting these results. Eddy-covariance studies do not provide information on spatial variation in the landscape and assume that the net flux of C is homogeneous over large areas (the so-called flux footprint). Obtaining spatially replicated data using this technique is costly and probably not feasible in many research sites over the tropics.

Interpreting data from ground-based measurements using permanent plots can also be problematic (Clark 2004). Using a large set of permanent plots over the tropics, Phillips et al. (1998) hypothesized that mature neotropical forests are acting as considerable carbon sinks. This hypothesis has been challenged (Clark 2002) due to problems associated with the dataset (however see Phillips et al. 2002). In a reanalysis of this dataset addressing previous critics, Baker et al. (2004) reached the same conclusions as in their previous analysis (Phillips et al. 1998), specifically they infer a net C uptake of the ecosystems solely from changes in aboveground biomass. From theory, the net accumulation of C in a forest ecosystem is accounted for by net ecosystem production (NEP) which includes inputs (gross primary production, GPP) and outputs (ecosystem respiration, ER) from the system (Landsberg and Gower 1997, Sala and Austin 2000, Chapin et al. 2002, Randerson et al. 2002, Chapin et al. 2006). Unfortunately, the analysis of the neotropical plots only estimated the input of C. The magnitude of respiratory C losses from these plots is uncertain. In addressing this problem Rice et al. (2004) showed that the inclusion of losses due to decomposition of coarse woody debris (CWD) largely offset the fixation of C in the processes of growth and recruitment.

However, the analysis of Rice et al. (2004) did not include losses from soil respiration which might be highly important in the total budget (Raich and Schlesinger 1992, Chambers et al. 2004).

Modeling experiments suggests that mature tropical forests can respond with high C fluxes to external forcing such as in climate and atmospheric CO_2 (Tian et al. 1998, Cramer et al. 2001, Clark et al. 2003). However, modeling results also appear to be highly uncertain and contradictory (Clark 2004), and there is generally no experimental evidence that corroborates specific model predictions.

The debate of whether tropical forests are C sources or sinks has been limited by the lack of a common conceptual framework for hypothesis testing. Research published to date is not consistent about the type of flux that should be measured and the spatial and temporal scope of inference allowed by the data. Lovett et al. (2006) and Chapin et al. (2006) have proposed the concept of NEP as a common term for multi-scale comparison of measured fluxes. Under this framework we propose a common set of hypotheses to test the role of mature forests in the ecosystem carbon balance using annual observations of NEP.

A null hypothesis to assess external forcing on carbon fluxes

Eugene P. Odum described the theoretical flows of energy in ecological systems during different stages of ecosystem development (Odum 1969). In his model, a mature ecosystem reaches a stage in which production and respiration are balanced, i.e. NEP = 0. During previous successional stages production and respiratory fluxes are highly

imbalanced. For this reason mature ecosystems are a good model system to test hypotheses about external forces such as climate change that might disrupt this balance by increasing or decreasing GPP or ER.

Odum's model is probably our best theoretical understanding of how ecosystems should work at maturity without any changes in external forcing. Alternative models of ecosystem development (Bormann and Likens 1979, Shugart 1984) as well as observational studies (Campbell et al. 2004) agree with Odum's predictions. A good candidate null hypothesis to test the effect of changes in external forcing on carbon fluxes would be that NEP = 0. However, we know that processes such as mortality, recruitment, competition, as well as inter-annual climatic fluctuations, introduce spatial and temporal variations in carbon fluxes that are propagated to the net flux. We hypothesize that NEP in mature ecosystems fluctuates around zero with an associated probability distribution. For this reason we propose the following null and alternative hypotheses to test the effects of external forcing on the net carbon flux of a mature ecosystem:

$$H_0: \quad NEP \in \theta, \qquad \theta = [-1.96\sigma, 1.96\sigma] \tag{1}$$
$$H_1: \quad NEP \notin \theta$$

We hypothesize that the average $NEP \sim N(0, \sigma^2)$ over the long term (multiple years) according to the Central Limit Theorem (Mukhopadhyay 2000). Note that these hypotheses are framed in Bayesian terms. Within this framework we can test the null hypothesis that the net carbon flux of the ecosystem is within *a priori* defined range of

variation (θ). This range can be subjective and defined by specific mechanisms such as forest stand dynamics, long-term disturbances, or inter-annual climatic variations. Evidence against the null hypothesis would suggest that other factors such as climate change or anthropogenic disturbances are forcing the ecosystem outside its expected range of natural variation.

In this study we evaluated NEP in a mature tropical forest of the Porce region in Colombia, using the hypotheses described above. We used an ecosystem carbon model to define a hypothetical range of natural variation of the net carbon flux caused by processes such as recruitment, growth, mortality, and decomposition. This range was compared against observational data of different carbon fluxes measured in the ecosystem.

Methods

Data for this analysis was collected at the Porce region in Colombia (6º45'37'' N, 75º06'28'' W). Mean annual precipitation is 1927 mm and mean annual temperature is 22.7ºC, with a monthly minimum of 21.3ºC and maximum of 24.1ºC. Altitude ranges from 900 to 1500 m in the transition from lowland to premontane tropical rain forests. Soils are derived from granitic rocks, have low fertility, and high acidity. Entisols and ultisols are the main soil orders found in the area (Jaramillo 1989).

Thirty three permanent plots (20 m x 50 m) were established in this forest (see Chapter 2). All trees, lianas and palms ≥ 10 cm in *D* (diameter at breast height or above irregularities) were measured in these primary forest-plots. Additionally, plants ≥ 1 cm in

D were measured in one subplot (10 m x 10 m) per plot. The total sampling area was 3.3 ha. Diameters were measured using conventional calipers for plants ≥ 10 cm, and digital calipers for plants $10 > D \geq 1$ cm. For buttressed trees its *D* was measured above the highest buttress.

Radial increments were measured to each tree > 10 cm *D* using dial-gauge dendrometers (Daubenmire 1945). Three 3-inch-nails were installed in each tree to provide support for the dendrometer. Trees $1 < D < 10$ cm were remeasured using digital calipers. Plot establishment and initial measurements were conducted between November 1999 and August 2000. All plots were remeasured at approximately one-year interval between November 2000 and May 2001. Between November 2001 and November 2002 all plots were measured again, thus completing a second one-year interval.

Biweekly observations of fine litterfall were conducted in the selected sampling plots. Twenty-eight litterfall traps (0.5 m^2) were installed in two sampling plots (14 traps each) in December 1999. Twenty additional traps were installed in February 2001. The complete measurement period extended from December 1999 to November 2003. Coarse litterfall was sampled in subplots (10x10 m) for the same time period and same frequency (Herrera 2000, unpublished data), (Agudelo and Aristizábal 2003, Moreno 2004).

Fine root production was measured using the ingrowth core method (Bohm 1979). Two plots were used to install seven ingrowth core sets (0-15 cm, 15-30 cm) per plot for two six-month periods. This experiment was conducted between January 2000 and January

2001. A second experiment was installed from September 2001 to May 2003. In the second experiment ingrowth cores were sampled every two months, approximately (Sierra 2004).

The litterbag method (Harmon et al. 1999) was used to estimate decomposition rates of fine litter in two of the sampling plots. Two experiments were performed. The first experiment was conducted between January 2000 and January 2001 and the second between February 2001 and May 2002 (Berrouet and Loaiza 2003). A simple exponential decomposition model (Olson 1963) was fit to the data to estimate the decomposition rate (*k'*). Decomposition rate of coarse woody debris was estimated using a time-series approach (Harmon et al. 1999) for one year. A set of 400 pre-weighted pieces of wood of different sizes from three different species were placed on the ground and collected at regular intervals. Decomposition rate constants were calculated as the proportion of weight lost.

Soil respiration was measured in six plots using a LI-COR soil respiration chamber (Li-6000-09, LI-COR Inc, Lincoln NE, USA) connected to a LI-COR portable photosynthesis system (Li-6200). Within each plot, paired subplots (2 x 2 m) were established to measure total soil respiration and heterotrophic respiration separately. The trenching-plot technique (Hanson et al. 2000) was used to measure heterotrophic respiration by excluding the growth of any living plant within the subplot. Measurements were conducted from October 2001 to June 2002. We extrapolated soil respiration to our first sampling campaign (approximately between January 2000 and May 2001) using the

relationships between temperature and soil moisture developed by Moreno (2004) for this site.

Annual estimates of NEP* were obtained by processing the information collected from the sampling plots. The following conceptual model was used to estimate net ecosystem production (after Chapin et al. 2006)

$$\text{NEP} = \text{GPP} - \text{ER} = (\text{NPP} + \text{Ra}) - (\text{Ra} + \text{Rh})$$

$$\text{NEP} = \text{NPP} - \text{Rh}, \quad (2)$$

where Ra is autotrophic respiration, NPP net primary production, and Rh heterotrophic respiration. Net Primary Production was calculated using the approach proposed by Landsberg & Gower (1997):

$$\text{NPP*} = \Delta W + w_{\text{det}} + w_{\text{herb}}\ , \quad (3)$$

where ΔW is total biomass increment, w_{det} is total detritus production, and w_{herb} is herbivore consumption. In this study we distinguish between the conceptual and the measured flux using an asterisk sign (*) for the latter. Data to estimate w_{herb} was not directly measured in the plots. However, entomological studies conducted by Giraldo & Bedoya (unpublished data) in the area present a rough estimate of leaf herbivory by ants. These authors estimated annual herbivory rates as 16% of leaf standing biomass. We used this rate to calculate herbivory consumption by ants during the two intervals studied.

Biomass increment (ΔW) was calculated using the procedure proposed by Clark et al. (2001a):

$$\Delta W = (\Sigma \text{ Increments of surviving trees}) + (\Sigma \text{ Increments of ingrowth}) \quad (4)$$

ΔW includes biomass change above- and belowground. Local biomass equations reported in Chapter 2 were used to calculate biomass of each individual. Biomass change was the difference of the estimated biomass for two consecutive measurements. Fine root biomass increments were added to plot biomass increments. Detritus production was calculated as annual fine litterfall measured in the plots.

Heterotrophic respiration associated with soil organic matter (SOM) was separated from respiration of the litter layer ($Rh^* = R_{SOM} + R_{det}$). Our estimations of heterotrophic respiration obtained from the trenched plots were used as R_{SOM}. Heterotrophic respiration from litter was calculated as

$$Rh_{litter} = SL * (1- \exp(-k')) \quad (5)$$

Where k' is the decomposition rate-constant from an exponential decomposition model and SL is standing litter. Alternatively, we used our litterfall data to compute decomposition rates assuming that the system is in steady state (k = fine litterfall/SL) (Olson 1963):

$$Rh_{litter} = k * SL \quad (6)$$

Uncertainty analysis

The uncertainty in our estimations was assessed by performing a Monte Carlo procedure. In this procedure we defined prior probabilities for the parameters of each component of NPP* and Rh* based on the results from our measurements. These *a priori* probabilities include uncertainty associated with measurement errors and spatial variation. Measurement errors are associated with the sampling procedure used. Uncertainty associated with spatial variation is obtained by differences in topography and soils over the landscape, as well as heterogeneity in canopy cover introduced by gap dynamics. Multiple estimations (10,000) of NPP* and Rh* were computed by randomly sampling the parameter space of the *a priori* probabilities. *A posteriori* probabilities (frequency distributions) from the outcomes were obtained and their standard deviation was used as a measure of uncertainty. The 95% confidence intervals for NPP*, Rh* and NEP* were calculated using these standard deviations.

We tested the effect of correlation between variables in our uncertainty analysis. According to statistical theory, the variance (σ^2) of two random variables A and B is propagated to a third variable $C = A + B$ by the expression $\sigma_C^2 = \sigma_A^2 + \sigma_B^2 + 2\,\mathrm{cov}_{AB}$. We used the Monte Carlo procedure to model the effect of correlation between variables. Two extreme scenarios were tested: complete correlation and complete randomness between all fluxes. Neither of these scenarios is very realistic but they provide boundaries

to constrain our estimation of variances. A third and more realistic scenario was tested, partial correlation between production and respiratory fluxes assuming a correlation of 50% between them. The coefficient of variation (CV) of the net flux was estimated for the ratio NPP*:Rh* instead of NEP* because the closer the average NEP* is to zero the larger the estimate of the CV. We avoided this shortcoming by estimating the CV on the NPP*:Rh* ratio which should be close to 1 for mature ecosystems (Odum 1969).

Calibration of the carbon model STANDCARB

We used the ecosystem carbon model STANDCARB version 2 (Harmon and Domingo 2001, Harmon and Marks 2002) to assess the range of variation θ of NEP due to stand dynamics for this forest. Specifically, we expect that the dynamic nature of mortality and regrowth will produce short term variation in the carbon balance at the ecosystem scale. STANDCARB 2 is a simulation model of living and dead C pools of forest stands. This is a hybrid model that incorporates features of a gap model with an ecological process model. The effects that tree species, succession, and regeneration have on carbon dynamics can be examined with this model. The spatial scale is restricted to the stand and stochastic processes are included.

STANDCARB was calibrated for the study site using parameters from the literature and local information. Five different groups of species were simulated simultaneously: early successional, late successional, palms, and gap species. Predictions of carbon stocks with this model were compared against our estimations for primary and secondary forests

(Chapter 2). Details about model parameterization for this study site are given in Chapter 3.

The model was run five times to obtain a representation of variation in carbon dynamics given the stochastic framework of the model. NEP was calculated from the output of total carbon stores for the interval 500-1000 years. During this interval the modeled ecosystem reached a steady state in all simulations where carbon stores plateau. The variance of NEP was calculated from the five simulations for the 500 year period (n = 2500 observations).

Hypothesis testing

To test the hypothesis posed in equation (1) we estimated the posterior probability of NEP given the observed NEP* data. This posterior probability was estimated applying the Bayes' theorem (Gelman et al. 2000):

$$P(NEP \mid NEP*) = \frac{P(NEP* \mid NEP)P(NEP)}{\int P(NEP* \mid NEP)P(NEP)dNEP}. \quad (7)$$

The prior probability of *NEP* was estimated from STANDCARB's output. The likelihood function of the observed data given the null hypothesis ($P(NEP*|NEP)$), as well as the integral in a possible range of *NEP* between -5 and 5 Mg C ha^{-1} y^{-1}, was estimated using the statistical software R 2.1.1 (Ihaka and Gentleman 1996).

The posterior probability was evaluated over the space of the null and alternative hypotheses (Mukhopadhyay 2000):

$$\alpha_0 = \int_{NEP \in \theta} P(NEP|NEP^*)dNEP, \qquad \alpha_1 = \int_{NEP \notin \theta} P(NEP|NEP^*)dNEP$$

We consider α_0 and α_1 posterior evidence in favor of H_0 or H_1, respectively. Specifically, if $\alpha_0 < \alpha_1$ the null hypothesis will be rejected (Mukhopadhyay 2000).

Results

*NPP**

The major components of NPP* measured during the two intervals were biomass increments of surviving trees and fine litterfall (Figure 3.1, Table 3.1). For the first interval the increment of survivors was 11.68 ± 0.96 Mg ha^{-1} yr^{-1}, and for the second interval 13.07 ± 1.64 Mg ha^{-1} yr^{-1}. Fine litterfall was 10.74 ± 0.58 Mg ha^{-1} yr^{-1} for the first interval, and 10.23 ± 0.47 Mg ha^{-1} yr^{-1} for the second interval. Biomass increments due to ingrowth were relatively small compared to increments of surviving trees. During the second interval a reduction in biomass increments of ingrowing trees was observed. Increments of ingrowth were 2.44 ± 0.65 and 0.11 ± 0.05 Mg ha^{-1} yr^{-1} for the first and second interval, respectively. Larger biomass increments were observed for trees rather than for other life forms such as palms and lianas (Table 3.1).

Estimated fine root production increased between the two intervals. The average fine-root biomass production was estimated as 2.65 ± 1.45 Mg ha^{-1} yr^{-1} during the first interval, and 4.87 ± 1.15 Mg ha^{-1} yr^{-1} during the second interval. This change in increment of fine root production was not associated with a similar change in the increment of leaf

production. Fine litter fall was estimated as 10.74 ± 0.58 Mg ha^{-1} yr^{-1} during the first interval and 10.23 ± 0.47 Mg ha^{-1} yr^{-1} during the second interval.

Herbivory was the smallest flux estimated and only accounted for 1.5 % of total NPP*. Our estimate of herbivory for the two intervals was 0.43 ± 0.22 Mg ha^{-1} yr^{-1}. This estimate was nearly constant for the two intervals because standing leaf mass also remained relatively constant; changing from 2.70 Mg ha^{-1} during the first interval to 2.69 Mg ha^{-1} during the second interval.

Uncertainty bounds were higher for fine roots and increments of surviors than for the other NPP* components (Figure 3.1, Table1). Small sample size was the main factor contributing to the observed uncertainty for fine roots. The uncertainty observed for the increment of surviving trees was probably the combination of spatial variation and the size of the pool. Larger pools showed larger absolute variation.

Net primary productivity was estimated as 12.59 ± 0.90 Mg C ha^{-1} yr^{-1} for the first interval and 12.93 ± 0.96 Mg C ha^{-1} yr^{-1} for the second interval. There was not a significant difference between these two estimates (p-value = 0.80 from a t-test).

Heterotrophic respiration

Decomposition rates estimated using the litterbag method were different between the two intervals. For the first interval k' was 0.89 ± 0.03 yr^{-1} and for the second interval it was 0.34 ± 0.08 yr^{-1}. Using the steady-state method, decomposition rates (k) for the first and

second intervals were 1.79 ± 0.17 yr^{-1} and 1.68 ± 0.30 yr^{-1}, respectively. Decomposition rates are more consistent between intervals using the steady-state method because litter fall rates are almost the same between the two intervals (Figure 3.1) and fine litter mass also remained relatively constant during the two intervals. Standing fine-litter mass in this forest was estimated as 6.03 ± 0.45 Mg ha^{-1} for the first interval and 6.23 ± 0.99 Mg ha^{-1} for the second interval (Chapter 2). Due to the fact that litterfall and standing litter remained relatively constant it is very likely that decomposition rates also remained constant. Differences between litterbag materials between the two intervals may have been associated with the differences observed in decomposition rates. For this reason we used decomposition rates estimated with the steady state method in further calculations. Consequently, fine litter respiration was equal to fine litterfall for the two intervals.

Respiration of CWD increased from 1.04 ± 0.62 Mg C ha^{-1} yr^{-1} in the first interval to 2.52 ± 1.69 Mg C ha^{-1} yr^{-1} during the second interval (Figure 3.2). Average dead coarse-wood mass changed dramatically between the two intervals due to an increase in mortality, especially of large trees. For the first interval, CWD mass was 8.74 ± 1.55 Mg ha^{-1} and for the second interval it increased to 20.86 ± 6.72 Mg ha^{-1}. The decomposition rate for coarse wood was estimated as 0.27 ± 0.30 yr^{-1}. Although this rate was only measured during the second interval we used it in our calculations for both intervals (notice the high variation of this decomposition rate which is due to the small sample size and the averaging effect of different coarse wood sizes).

Our estimates of soil respiration were associated with large uncertainties mainly due to the small sample size used. During the first interval soil respiration was -6.36 ± 1.94 Mg C ha^{-1} yr^{-1} and for the second interval it was -7.98 ± 0.29 Mg C ha^{-1} yr^{-1}. Uncertainty bounds for soil respiration in the first interval were higher because this flux was predicted in part from measurements taken during the second interval.

Carbon losses due to heterotrophic respiration were estimated as -12.26 ± 2.05 Mg C ha^{-1} yr^{-1} and -15.07 ± 1.70 Mg C ha^{-1} yr^{-1} for the first and second intervals, respectively. The major component of heterotrophic respiration was soil organic matter respiration (approximately 52% on average) which is also the major driver of the final uncertainty during the first interval. For the second interval an important source of uncertainty was introduced by the observed mortality of large trees which was propagated from the coarse wood pool to our estimate of heterotrophic respiration.

*NEP**

Correlation between fluxes has an important effect on the estimate of uncertainty in net carbon flux (Table 3.2). Assuming complete randomness the uncertainty of the average NPP*:Rh* ratio was as high as 19.7% while assuming complete correlation this uncertainty dropped to 7.7%. Assuming 50% correlation between production and respiration the uncertainty of the net flux was estimated as 11%. We used our estimate of uncertainty from the partial correlation scenario in our subsequent examination of uncertainty for the first and second intervals, given that much of the forest production replaces litterfall and mortality.

Net ecosystem production was estimated as 0.34 ± 1.15 Mg C ha^{-1} yr^{-1} for the first interval. The uncertainty analysis showed that NEP* for the first interval may have ranged between -1.88 and 2.59 Mg C ha^{-1} yr^{-1} (95% confidence limits). NEP* for the second interval was estimated as -2.15 ± 0.76 Mg C ha^{-1} yr^{-1} with 95% confidence limits between -3.75 and -0.61 Mg C ha^{-1} yr^{-1} (Figure 3.3).

Combining the results from the first and second interval we found a possible range of variation of NEP* between -4.03 and 2.22 Mg C ha^{-1} yr^{-1} (Figure 3.4), which includes uncertainty in the estimates as well as spatial and temporal variation.

Simulations of carbon fluxes from STANDCARB

Our simulations of NEP from STANDCARB (Figure 3.5a) followed the theoretical pattern for ecosystem development (Odum 1969). The minimum and maximum values of NEP for mature forests predicted by the model were -4.36 and 1.24 Mg C ha^{-1} yr^{-1}, respectively. This range includes larger negative than positive values but the probability of large emissions was low (Figure 3.5b). Large negative pulses are due to mortality events and subsequent decomposition, which is in general faster than biomass recovery. The mean and median NEP estimated from these simulations were -0.015 and 0.14 Mg C ha^{-1} yr^{-1}, respectively. The expected (and subjective) natural variation ($\hat{\sigma}^2$) of NEP was estimated as 0.60 Mg C ha^{-1} yr^{-1}. This variation is basically the result of the interaction of ecosystem processes such as recruitment, growth, mortality, and decomposition of the

five species-groups simulated. The effects of climatic variations were not included in these simulations, but would have increased the degree of natural variation.

From these results we hypothesize that $\theta \sim N(0, 0.60)$. The assumption of normality implies that the expectancies of NEP are made over long term averages. We hypothesize a mean of zero because it is the theoretically expected value for NEP in any mature ecosystem (Odum 1969) and close to STANDCARB predictions.

Testing the null hypothesis

The prior probability interval (95% probability) for NEP calculated from STANDCARB outputs was -1.51 to 1.51 Mg C ha^{-1} yr^{-1}. Our posterior probability for NEP given the observed data NEP* was estimated within the prior range (Figure 3.6), therefore our estimate of $\alpha_0 = 1$. From this analysis no evidence against our posed null hypothesis was found.

Discussion

In an extensive literature review of NPP* data in tropical primary forests, Clark et al. (2001b) found that past studies were usually limited to one or two components of aboveground NPP. In our study we included changes in biomass above and belowground as well as litterfall, herbivory, and fine root production. For this reason our estimates of NPP* are among the highest reported for tropical forests. In forests with relatively similar biomass to our study site, total NPP* can be found between 6.0 and 21.7 Mg C ha^{-1} yr^{-1} according to Clark et al. (2001b). The range for NPP* in our site was between 10.9 and

14.6 Mg C ha^{-1} yr^{-1} suggesting that this site has intermediate productivity compared to other tropical forests with the same biomass. Comparing our results with the temperature-productivity relationship reported by Clark et al. (2001b) these forests are in the upper range of productivity relative to other forests with the same temperature.

Uncertainty of measured fluxes

Changes in biomass were the most important components of total uncertainty in NPP* (Figure 3.1). Although ecosystem models of succession predict little variation in biomass change for mature forests other factors, such as soil characteristics and species composition, are important drivers of spatial variation in biomass accumulation. We observed large variations of changes in biomass across the landscape, larger than the variations between observational periods. Although we did not observe an important change in the average NPP* during the two intervals, changes in the relative importance of some components were observed. For example, in the second interval we observed a decrease in the average biomass change of the ingrowth and an increase in the average fine root production.

The large uncertainties observed in soil respiration were probably a consequence of the small sample size used and the large size of the flux. Larger fluxes are generally more variable and also often more difficult to measure. We estimated that it would be necessary to measure soil respiration on at least ten plots to decrease the coefficient of variation of the average below 20%.

The mortality events observed during the second interval were very important in causing an additional source of uncertainty in the respiratory flux. During the first interval we were unable to capture that uncertainty in our measurements. It is likely that other temporal processes such as pest outbreaks or droughts were not captured in our observational timeframe. This study was mainly designed to capture the spatial variations over the landscape, thus the temporal variations remain relatively unexplored (although spatial variation provides a good representation of temporal variations as it is usually assumed in chronosequence studies).

Uncertainty of non-measured fluxes

We recognize that not all components of primary productivity as in Clark et al. (2001a) were measured in this study. Of total aboveground production we did not measure volatile and leached organics as well as other components of herbivory such as sap-sucking, frugivory, and herbivory of species other than ants. We found that leaf herbivory by ants only accounted for 1.5% of total NPP*, although Clark et al. (2001b) report larger proportions. It is likely that we have underestimated total herbivory; however we do not have a good representation of the magnitude of the total of this flux in the study site. Our personal observations, though, are consistent with the idea that ant herbivory is the major consumer flux in this forest. It is also likely that more herbivory only means higher Rh, so it is unlikely to impact estimates of NEP.

A likely range of VOC emissions in tropical forests has been reported as 0.15 to 0.31 Mg C ha^{-1} yr^{-1} by Clark et al. (2001b), based on modeling results reported by Guenther et al.

(1995), who found maximum VOC emissions of 4% of annual NPP. However, this range is highly uncertain (Guenther et al. 1995, Clark et al. 2001b). Recent research has shown that VOC emissions in tropical forests are highly seasonal (Andreae et al. 2001, Kuhn et al. 2004) as opposed to constant annual emissions assumed in previous modeling studies. Additionally, Kuhn et al. (2002) and Andreae et al. (2002) have found that the exchange of VOCs is bi-directional, i.e. that canopies in tropical forests can act as sinks (via reuptake) of some organic compounds such as short-chain volatile organic acids. Andreae et al. (2002) found consistent emission trends only for isoprene and monoterpenes at different sites in the Amazon. Monoterpenes contributed no more than 10-15% of the total isoprenoid flux. These results suggest that emissions of VOC are lower than previously thought, although they are highly dependent on variations of community composition over the landscape (Greenberg et al. 2004). Geron et al. (2002) found isoprene emissions ranging from 0.078 to 0.083 Mg C ha^{-1} yr^{-1} at La Selva, Costa Rica, and total VOC emissions probably did not exceed 0.1 Mg C ha^{-1} yr^{-1}. We believe that by not including VOC emissions in our calculations we underestimated NPP* by less than 1%.

Our budget did not include coarse root growth of palms and lianas. We only used root biomass equations for trees, but were unable to develop this type of equations for other life forms. This flux is probably not very large. The coarse root: shoot growth ratio of trees was about 0.27 for the first intervals. Applying this ratio to the aboveground growth of palms and lianas we found a possible underestimation of total growth of 0.31 Mg C ha^{-1} yr^{-1} for this interval.

Other belowground components of total NPP* that were not measured are the production of root exudates, exports to mycorrhizae, and root herbivory. We are not certain about the magnitude of these fluxes, but we measured the respiratory fluxes associated with these processes as part of soil heterotrophic respiration. Thus, our budget might be biased towards the respiratory component, although not all the C losses were accounted in the heterotrophic respiration flux. For example, from the respiratory losses, we did not account for decomposition of litter intercepted in the overstory. This flux is especially important for dead branches and mid-sized coarse woody debris that are being consumed by decomposers. Decomposition of intercepted fine litter does not affect the total budget because it is not being measured in the litterfall component.

Lateral carbon fluxes such as erosion and leaching were also omitted in our calculations. Leached organic compounds have been measured in other forests and small fluxes have been detected. At La Selva, Schwendenmann and Veldkamp (2005) found a DOC flux of 0.28 Mg C ha^{-1} yr^{-1} in the litter leachate. Similarly, a small flux of 0.58 Mg C ha^{-1} yr^{-1} was measured in a temperate rain forest in Western Oregon, USA (Lajtha et al. 2005).

Our omission of different components of the production and respiratory fluxes introduced uncertainty in our estimations of NPP* and Rh*, however most of these fluxes cancel out in the estimation of NEP*. We used the Monte Carlo procedure to estimate the uncertainty introduced by the exclusion of the fluxes mentioned above. Using the ranges reported in Table 3.3 we estimated an average underestimation of NPP* of the order of

0.77 ± 0.22 Mg C ha^{-1} yr^{-1}. Similarly, the underestimation of Rh* is of the order of -0.47 ± 0.18 Mg C ha^{-1} yr^{-1}. For NEP*, we predict an average underestimation of 0.30 Mg C ha^{-1} yr^{-1} ranging from -0.26 to 0.85 Mg C ha^{-1} yr^{-1}. This uncertainty is lower than the uncertainty associated with spatial and temporal variation observed during the two intervals studied.

This analysis showed that the estimation of NPP* and Rh* is consistent with the "complexity paradox" (Oreskes 2003) in ecological modeling. Recent models of NPP, Rh, and NEP (Clark et al. 2001a, Chapin et al. 2002, Randerson et al. 2002) stress the importance of including all carbon fluxes in the estimation of carbon budgets. This approach leads to a better description of complex processes. However, as more processes are included in the models more uncertainty occurs as measurement and estimation errors are propagated in to the final estimates (Figure 3.7). Some of the processes reviewed in this study that were not measured, added more uncertainty to the final estimates of NPP* and Rh* than the reduction of bias accomplished by their inclusion. Interestingly, most of these uncertainties and biases cancel out in the estimation of NEP*.

Implications for the carbon budget

Given the large uncertainties observed we did not find sufficient evidence to reject the null hypothesis that this ecosystem is outside the *a priori* defined natural range of variation. Although the observed uncertainty range includes values well outside the theoretical range of variation it also covers the complete range of possible theoretical values of NEP for a mature ecosystem. The observed uncertainty range is obviously

higher than the *a priori* natural variation because uncertainties in measurements and estimates are included.

Variations due to climate or long-term disturbance cycles were not included in our *a priori* defined range. For this reason this hypothetical range of variation is likely underestimated. To address this issue we compiled previous studies of carbon fluxes in tropical forests (Figure 3.8). Not surprisingly, the majority of previous studies were within our a priori defined range that only included variation due to gap dynamics. Only three studies were well outside this range (Figure 3.8). Fan et al. (1990) study was conducted over a very narrow period of time so the interpretation of this datum on an interannual basis is problematic. The highest measurements of NEE ever reported in tropical forests (Malhi et al. 1998, Loescher et al. 2003), were conducted during La Niña events of 1995-1996 and 1998-2000, respectively. However, the study reported by Rice et al. (2004) and this study were also conducted during the 1998-2000 La Niña and no large net fluxes were observed, suggesting that the effects of this large scale climatic variations differ geographically. However, it is clear from Figure 3.8 that large deviations of carbon fluxes in the tropics have been associated with extreme large scale climatic effects. Although it is not explicitly tested in this study, data from Figure 3.8 suggest that C fluxes associated with stand dynamics are in the same order of magnitude than fluxes associated with normal climatic fluctuations. This possible explanation of sources of variation remains little explored (however see Masek and Collatz 2006 for an example in North America) but could be tested by integrating models that only consider stand dynamics and models that consider climatic fluctuations.

The evidence obtained in this study is not sufficient to infer effects of systematic changes in external forcing on the carbon flux of this ecosystem, but this does not mean that there is no effect of anthropogenic disturbances. These forests are highly fragmented and processes such as community dynamics or microclimate are likely to be altered (Laurance 2004). Over the landscape, it would seem that fragmentation is not affecting the overall carbon flux, but it is also possible that the effects of fragmentation are masked by the uncertainties in our estimates. Effects of other important global processes such as increases in temperature and atmospheric CO_2 concentration are not possible to infer from this study.

Our results agree with recent studies of carbon dynamics in mature tropical forests (Saleska et al. 2003, Miller et al. 2004, Rice et al. 2004) that also found a neutral balance of these ecosystems with respect to the atmosphere. The estimates of carbon fluxes from Saleska et al.(2003), Miller et al. (2004), Rice et al. (2004), and partially Loescher et al. (2003) are within the prior probability range that we assumed for our study site (Figure 3.8). Our assessment of variation due to stand dynamics suggests that mature tropical forests might be oscillating within their expected range of natural variation. However, more observations are needed throughout the tropics to test this hypothesis. Observations over extreme climatic events would provide valuable information on the range of behavior of C fluxes.

The methodological framework for hypothesis testing proposed in this study can be very helpful to address the effect of global change on carbon dynamics since long-term observations are not strictly needed. Using *a prior* probability distribution it is possible to ask the question of whether or not the observed data is within an expected range of variation. This study shows that, a distribution of estimates is more important than the average NEP* for a given ecosystem, because it provides a range of variation that can be compared to a hypothetical range. If observational evidence against the null hypothesis is found we can be more certain whether an external factor is driving the ecosystem outside its expected range. Models are an important tool to set prior distributions of NEP because they are our best integrated representation of physiological and ecological processes that affect carbon dynamics.

Tables

Table 3.1. Changes in biomass of surviving and recruited individuals to the plots for the two intervals of study.

	Survivors		Ingrowth	
	Average ± SE	% of Total	Average ± SE	% of Total
2000-2001				
AGB[a] of Trees > 1 cm *D*	8.75 ± 0.87	75.0	1.43 ± 0.60	59.1
CRB[b] of trees > 1 cm *D*	2.31 ± 0.40	19.8	0.30 ± 0.14	12.4
AGB of Lianas	0.19 ± 0.06	1.6	0.08 ±0.05	3.3
AGB *O. bataua*	0.10 ± 0.03	0.9	0.28 ± 0.16	11.6
AGB of other palms	0.32 ± 0.10	2.7	0.33 ± 0.17	13.6
Total increment	11.67 ± 0.96	100	2.42 ± 0.65	100
2001-2002				
AGB of Trees > 1 cm *D*	9.87 ± 1.56	75.5	0.07 ± 0.06	63.6
CRB of trees > 1 cm *D*	2.70 ± 0.44	20.6	0.01 ± 0.001	9.1
AGB of Lianas	0.25 ± 0.06	1.9	0.001 ± 0.001	0.9
AGB *O. bataua*	0.22 ± 0.01	1.7	0	0
AGB of other palms	0.05 ± 0.02	0.4	0.02 ± 0.02	18.2
Total increment	13.08 ± 1.60	100	0.11 ± 0.05	100

[a] AGB: Aboveground biomass.

[b] CRB: Coarse root biomass.

Table 3.2. Effect of correlation in the estimate of uncertainty for each mayor flux. Results only for the first interval of study. Units in Mg C ha^{-1} yr^{-1}.

Scenario	NPP standard deviation	Rh standard deviation	NEP standard deviation	CV of mean NPP/Rh
Complete randomness	0.90	2.06	2.26	20.4%
Complete correlation	2.14	2.85	0.79	12.5%
Partial correlation	1.54	2.43	2.12	19.5%

Table 3.3. Hypothetical uncertainty bounds and their distribution for non-measured fluxes.

Pool	Distribution	Spread	Units
Production			
Herbivory	Uniform	Min = 0, max = 5.5	% of NPP
VOC	Uniform	Min = 0.5, max =1.5	% of NPP
CR increment of survivors of other life forms	Normal	Average = 0.07, sd = 0.01	Mg C ha^{-1} yr^{-1}
CR increment of ingrowth of other life forms	Normal	Average= 0.06, sd = 0.02	Mg C ha^{-1} yr^{-1}
Root exports	Uniform	Min= 0.5, max = 2.0	% of NPP
Losses			
CW mass intercepted undergoing decomposition	Uniform	Min= 5, max = 15	% of standing mass on the forest floor
DOC	Uniform	Min= 0.1, max = 0.7	Mg C ha^{-1} yr^{-1}

Figures

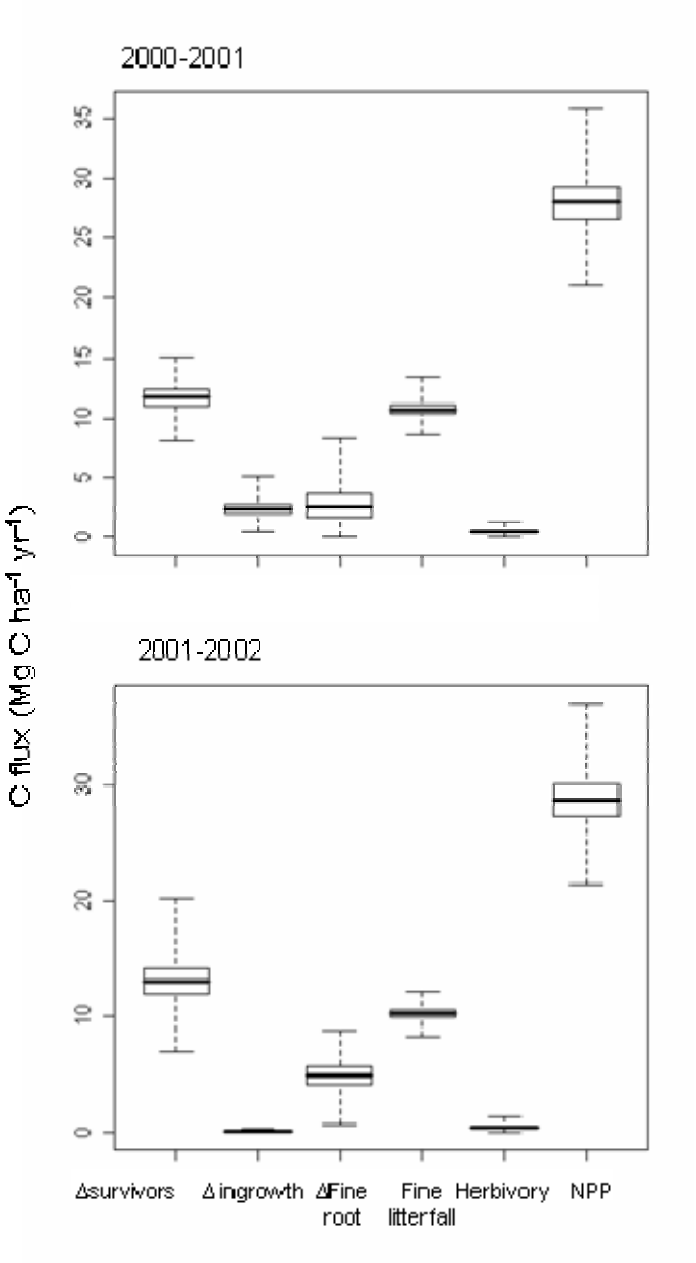

Figure 3.1. Box plots of each component of net primary production for the two measurement intervals (2000-2001 and 2001-2002). The plot was constructed with the outputs from the Monte Carlo simulations (10,000 observations). Boxes contain values between the 25 and 75 percentiles. Whiskers extend to the maximum and minimum values obtained from the simulation.

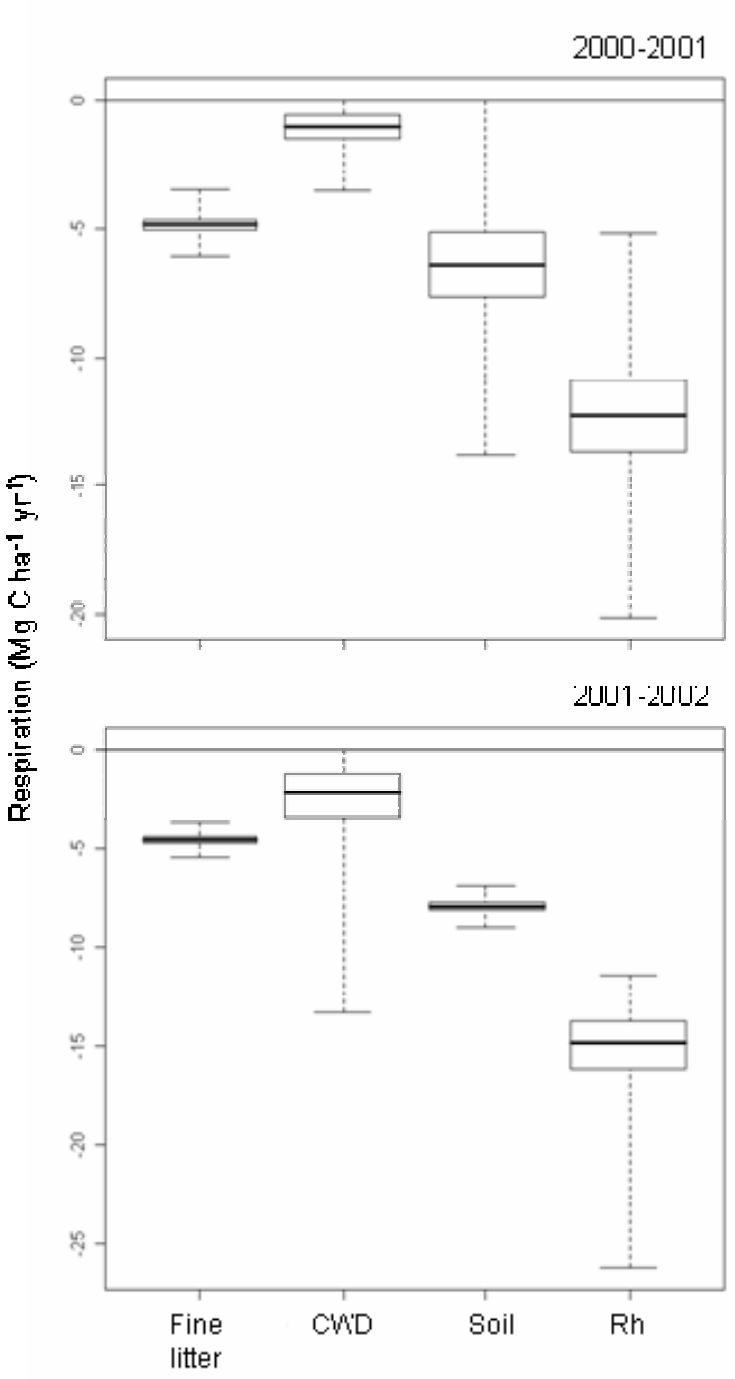

Figure 3.2. Box plots of each component of heterotrophic respiration for the two measurement intervals (2000-2001 and 2001-2002). The plot was constructed with the outputs from the Monte Carlo simulations (10,000 observations). The vertical line is the median, and the box includes 25 and 75 percentiles. Whiskers extend to the maximum and minimum values obtained from the simulation.

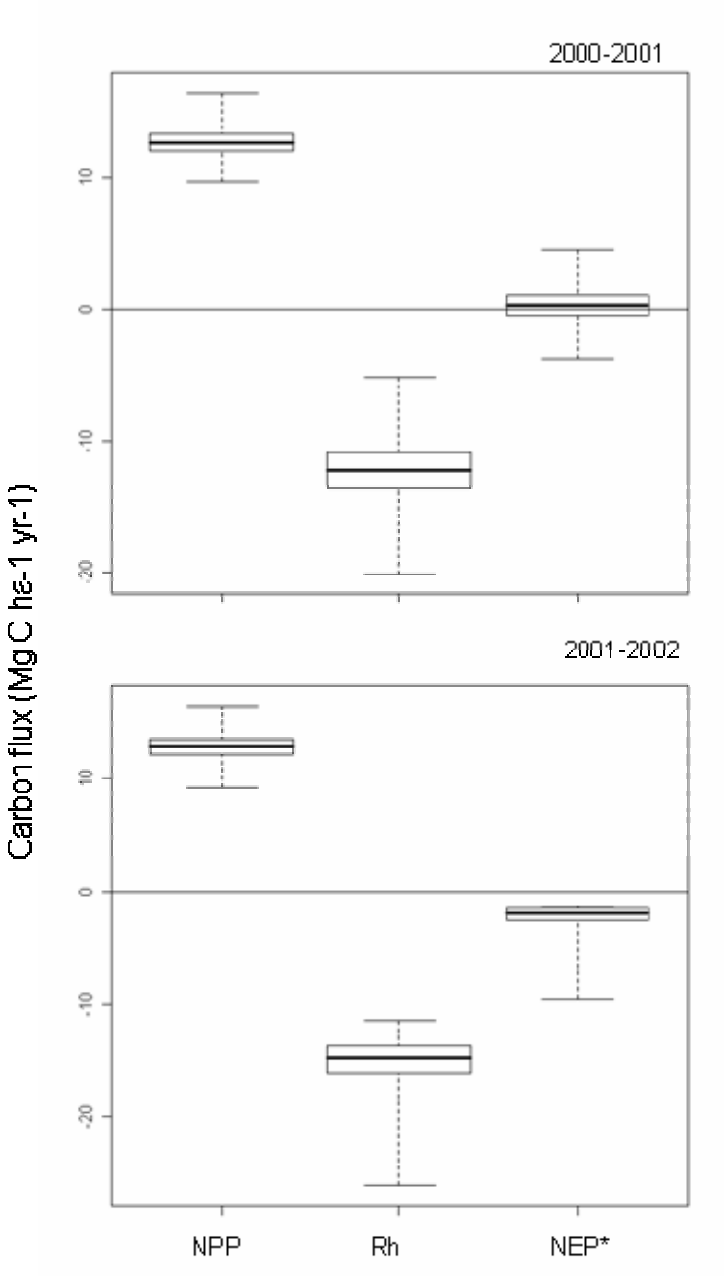

Figure 3.3. Box plots of each component of net ecosystem production for the two measurement intervals (2000-2001 and 2001-2002). The plot was constructed with the outputs from the Monte Carlo simulations (10,000 observations). The vertical line is the median, and the box includes 25 and 75 percentiles. Whiskers extend to the maximum and minimum values obtained from the simulation.

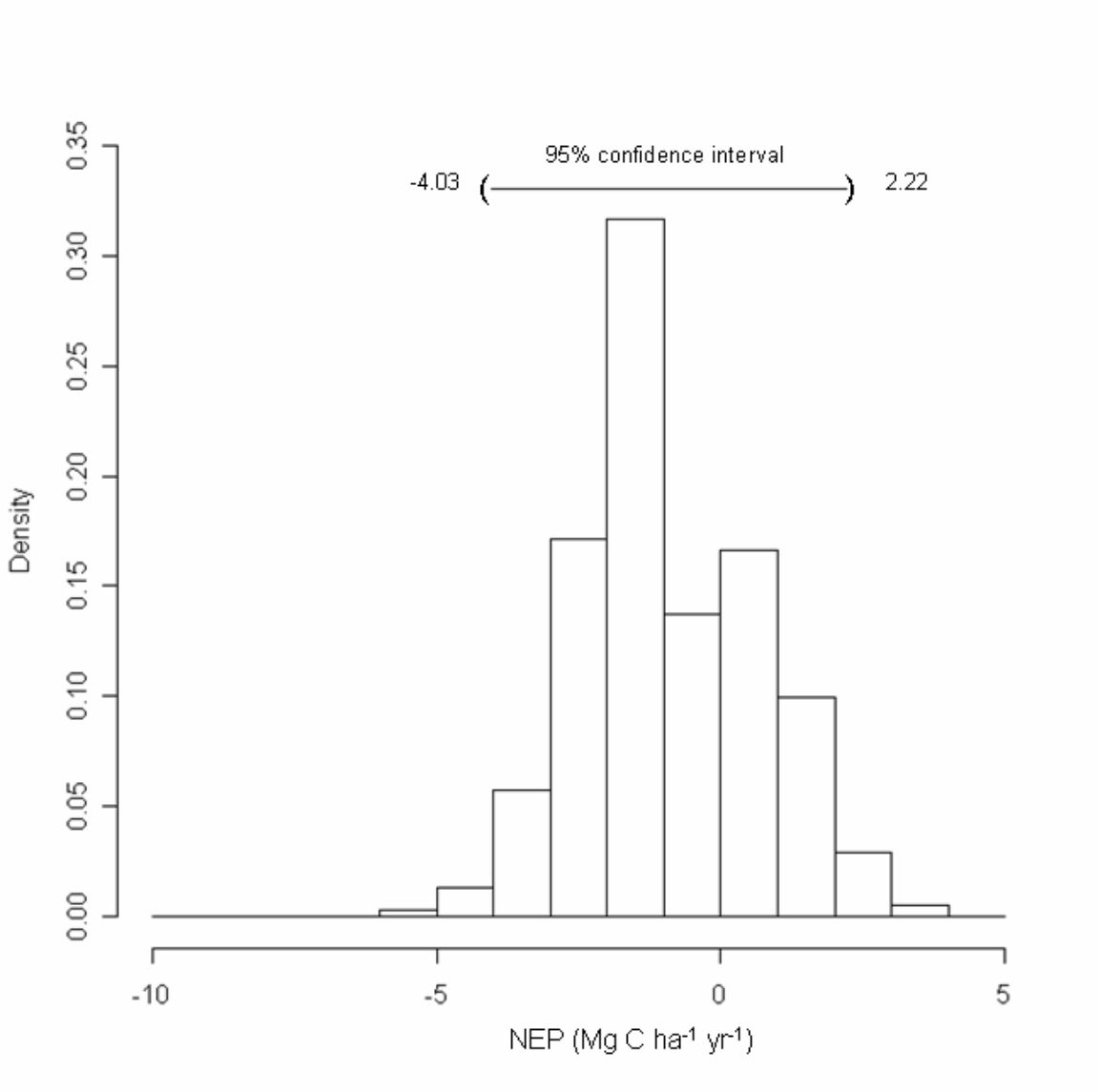

Figure 3.4. Histogram and 95% confidence interval of net ecosystem production for the two intervals from the observed data and the Monte Carlo simulations.

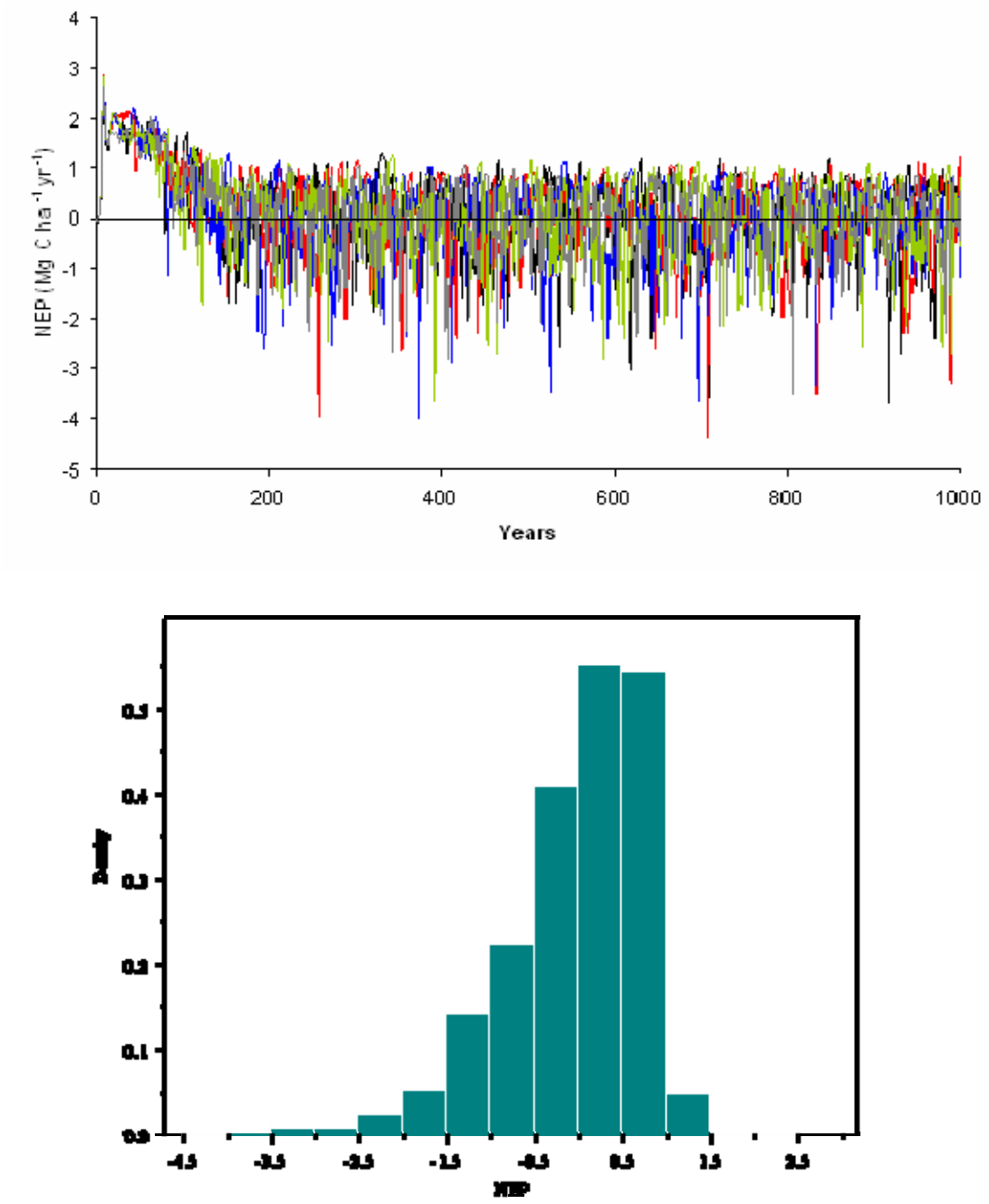

Figure 3.5. Results from STANDCARB simulations of net ecosystem production plotted against time (upper) and as histogram (lower). Colors in upper lines represent different simulations. The histogram only includes results from years 500-1000.

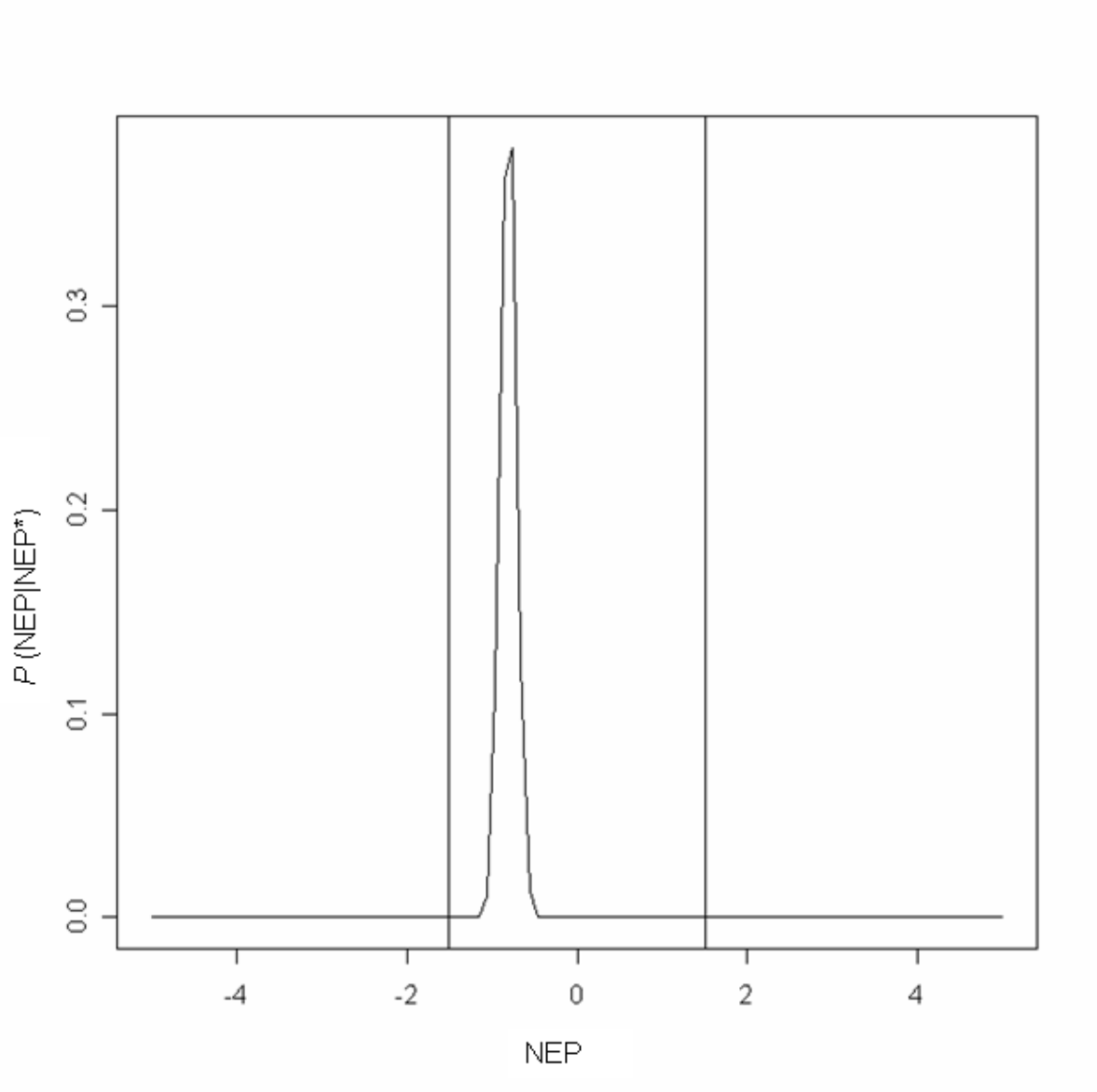

Figure 3.6. Posterior probability of NEP given the data NEP*. Vertical lines represent the 95% confidence interval of the prior distribution of NEP.

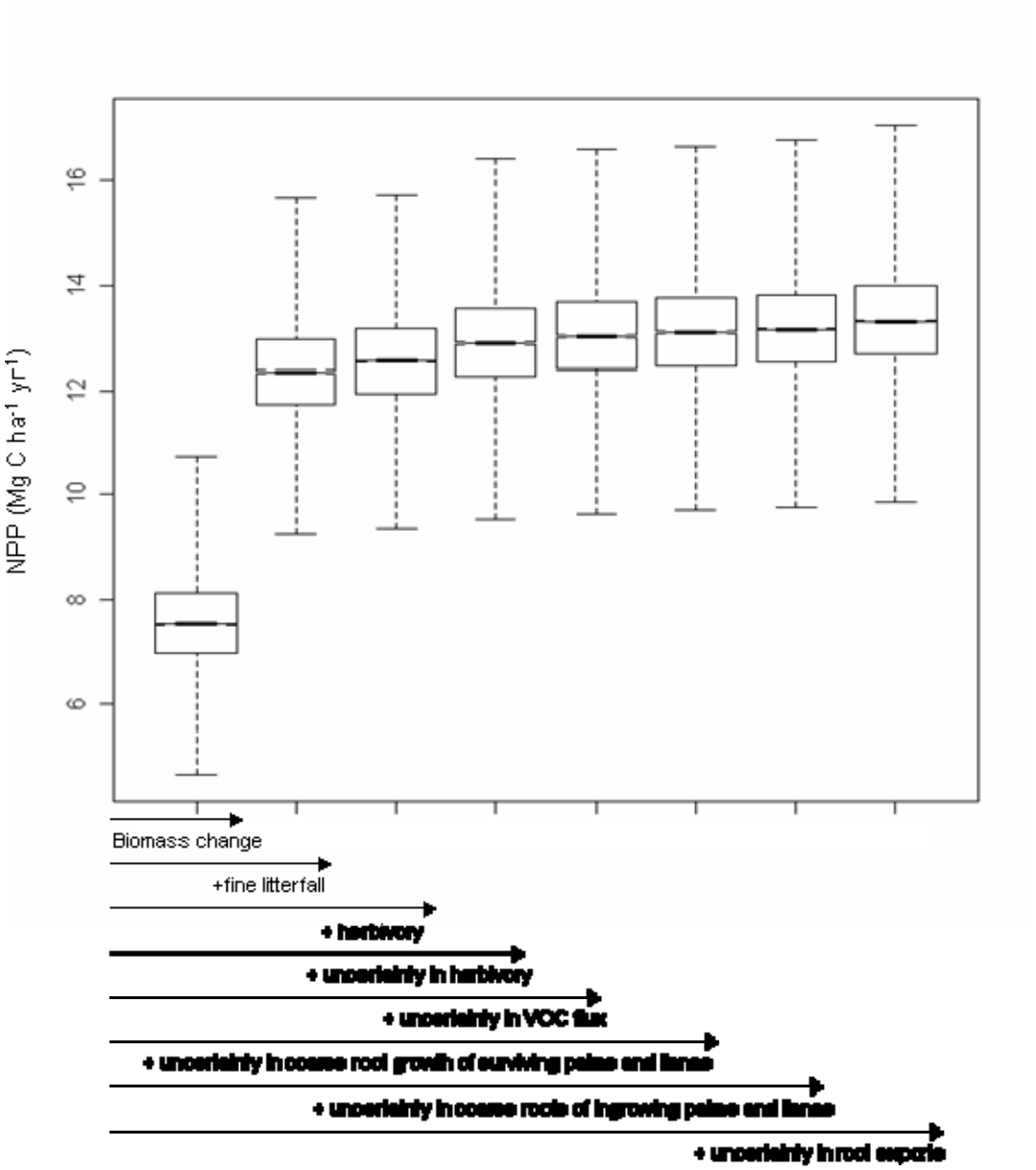

Figure 3.7. Effect of the addition of different fluxes in the estimation of NPP*. Labels in the x axes are: 1) biomass change, 2) 1 + fine litter fall, 3) 2 + herbivory, 4) 3 + uncertainty in herbivory, 5) 4+ uncertainty in VOC flux, 6) 5 + uncertainty of coarse root growth of surviving lianas and palms, 7) 6 +uncertainty of coarse root growth of ingrowing palms and lianas, 8) 7 + uncertainties in root export. Uncertainties calculated from Table 3.3.

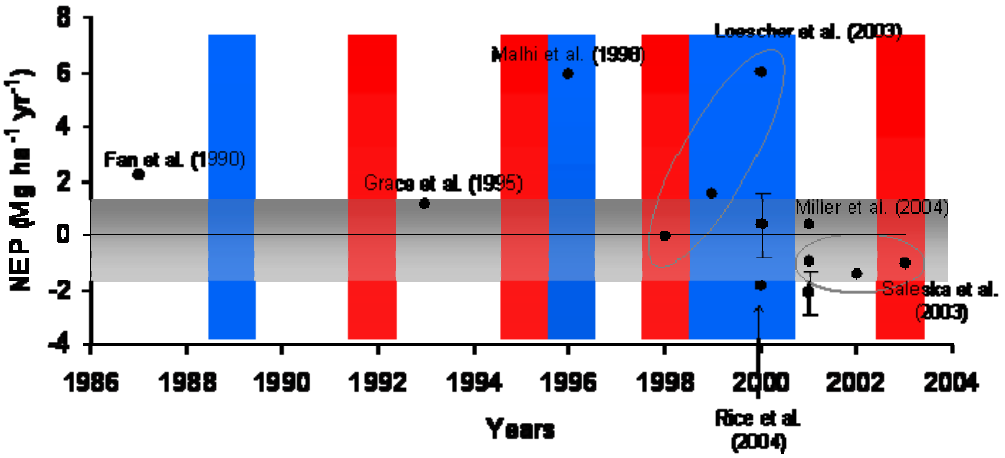

Figure 3.8. Previous carbon flux studies in mature tropical forests. Positive numbers refer to C sinks and negative numbers as carbon sources. Reported NEE data were transformed to NEP multiplying by -1. The two periods measured from this study include error bars. The shadow horizontal area is the a priori defined range from this study. Red bars represent El Niño years and blue bars La Niña years.

CHAPTER 4

EFFECTS OF PROCESSES AT THE POPULATION AND COMMUNITY LEVEL ON BEHAVIOR OF AN ECOSYSTEM CARBON MODEL

Carlos A. Sierra, Mark E. Harmon

Abstract

Processes at the level of populations or communities are often ignored in ecosystem carbon models. However, the degree to which these processes have important effects in carbon dynamics at the ecosystem level is not clear. The exclusion of population and community dynamics in ecosystem carbon models is based on several possible assumptions. For population dynamics it assumes: 1) colonization lags are minimal, and/or 2) variability introduced by variation in mortality completely dampens as temporal and spatial extent increases. Exclusion of community dynamics assumes either that: 1) the effects of species on ecosystem processes are the same for all species, or 2) the effect of species on ecosystem processes are different, but the mixture of species never changes over time, or 3) species effects on ecosystems are different and the species mixture changes over time, but the effects are not large enough to matter. In this study we asked the question of what behaviors emerge by introducing population and community dynamics in an ecosystem carbon model. To address this question we used STANDCARB, an ecosystem carbon model hybridized with a gap model that allows the study of population, community, and ecosystem dynamics. Our simulations showed that at the population level, colonization and mortality rates can limit the maximum biomass achieved during a secondary successional sequence. Colonization rates can introduce lags in the initiation of carbon accumulation and mortality rates can have important effects on annual variation in live biomass. Community dynamics, defined here as the replacement of species during succession, altered the mixture of species over time. With species having differences in ecosystem parameters, such as growth and mortality rates, community dynamics introduced patterns of carbon accumulation that could not be

reproduced using a single species with the average of parameters of multiple species or by simulating the most abundant species (common strategies employed in ecosystem models). We concluded that the assumptions for excluding population and community dynamics in ecosystem carbon models are not supported by our results or by previous research conducted on the topic. Exclusion of these dynamics therefore introduces uncertainty, however, the relevance of this uncertainty depends on the question being examined and the degree of resolution desired.

Introduction

Models have become a necessary tool to understand the carbon cycle because they integrate processes across spatial and temporal scales (Bugmann et al. 2000), and can be used to predict the consequences of environmental change on ecosystem function (Aber et al. 2001). Most of the success of ecosystem models in the study of the carbon cycle comes from the realization that biological systems are organized hierarchically and are subjected to the effects of environmental factors (Urban et al. 1987). The interaction between environmental drivers and elements of the system, as well as interactions among these elements, are difficult to describe without the use of models. In this sense, models are a useful tool to answer questions about the effects of the environment on ecosystem structure and function. This usefulness is evident by the wealth of literature about the possible effects of climate change on the carbon balance of different ecosystems (e.g. Bachelet et al. 2001, Cramer et al. 2001, Dullinger et al. 2004, Jones et al. 2005). Moreover, predictions and projections from these models are of high relevance in discussing policies to mitigate and adapt to climatic change.

The net carbon balance in forest ecosystems is represented within ecosystem models as the result of inputs from autotrophic production and outputs from ecosystem respiration (Aber and Melillo 1991). In ecosystem models, carbon enters the ecosystem through the process of photosynthesis, is allocated to different pools, and is respired at different rates from each of these pools. Although models differ in their mathematical representation of the processes of photosynthesis, allocation, and respiration, they all explicitly model these processes.

Many ecosystem models have a very detailed description of physiological processes involved in photosynthesis and allocation. Parameters used to model these processes are commonly obtained from laboratory experiments and field observations at small spatial and temporal scales (e.g., stomatal conductance measured during a day). However, model predictions are usually made over large areas such as biomes and for long time periods. This approach involves a scaling issue that has to be considered carefully because processes in intermediate levels of organization are ignored (see Bugmann et al. 2000). The issue of up-scaling from short-term measurements to long-term predictions has been discussed with some detail elsewhere (Harvey 2000, Reynolds et al. 2001, Bonan et al. 2002), whereas the omission of processes in intermediate levels of organizations such as populations and communities has been less studied.

Effects of species traits and population dynamics on ecosystem processes

Forest ecosystems contain populations of tree species which differ in attributes such as light requirements to establish and grow, capacity to fix nitrogen, life span, maximum height, etc. Population dynamics quantify the change in the numbers of individuals of a single species over time (Silvertown and Charlesworth 2001). The dynamics of a population is mainly determined by the number of births and deaths, which in turn can be influenced by climate, soil, pollinators, seed dispersers, the density of the population itself (intra-specific competition), and the density of populations of other species (inter-specific competition) (Silvertown and Charlesworth 2001).

Populations of different species often differ in traits that may have implications for ecosystem processes. For example, nitrogen fixers play an important role in the supply of nitrogen to ecosystems (Vitousek and Field 1999), however, the total supply of nitrogen will largely depend on the relative abundance of N-fixers relative to the other species present. Population dynamics may have important effects on ecosystem processes, because changes in population densities are directly associated with changes in the abundance of certain traits relevant to ecosystem function.

Plant species can have dramatic effects on ecosystem properties and processes such as soil chemistry and structure, primary productivity and evapotranspiration, and fluxes of trace gases (Huston and Gilbert 1996). It has been hypothesized that both, species identity and species number strongly affect the productivity of ecosystems (Loreau et al. 2001). In some ecosystems, high productivity is found where one or two species are dominant (Huston 1979, Huston and Gilbert 1996). Similarly, manipulative experiments in grasslands have found that species richness is positively correlated with total biomass (Loreau et al. 2001). It also has been hypothesized that species number is correlated with ecosystem stability (Tilman 1996, McCann 2000). It is important to note that most of the experimental-based research developed in this topic has been conducted in grassland ecosystems (Sala et al. 1996, Hector et al. 1999, Tilman et al. 2001) where the manipulation of diversity can be relatively easy in comparison to forest ecosystems. A larger diversity in functional attributes can be found in forest ecosystems, but little is know experimentally about the relationship between diversity and ecosystem function in these systems.

Role of community dynamics in influencing ecosystem processes

Populations coexisting in an ecosystem define a community (Chapin et al. 2002). The process of succession is characterized by a relatively continuous replacement of populations (i.e., community dynamics) with different ecological traits. Contrary to changes in species composition, the sequence of processes during succession, as well as changes in general aspects of structure, are quite predictable (Peet 1992, Guariguata and Ostertag 2001, Rees et al. 2001, Franklin et al. 2002). For example, after the abandonment of agricultural lands in the tropics, light demanding species such as herbs, grasses and ferns are the first colonizers persisting for the first one to five years. Short-lived pioneers, commonly N-fixing legumes, replace the initial colonizers. After 5-20 years the short-lived pioneers are gradually replaced by long-lived pioneers and shade-tolerant tree species (Guariguata and Ostertag 2001). These different groups of species may have different traits that potentially can affect the C flux within the ecosystem. Short-lived pioneers often have low wood density, high mortality, and short life-span, which affect the amount of C that can be accumulated and released during the first stages of succession. Shade tolerant species show a contrasting behavior, accumulating C at a slower rate and also releasing it more slowly during the decomposition process. Thus, community dynamics may involve a variety of changes in processes that have relevance in controlling the rates of carbon accumulation and release in forest ecosystems.

Gap and hybrid models

Models that explicitly address population and community dynamics are commonly known as gap or patch models, and are often derived from the JABOWA model (Botkin et al. 1972, Shugart 1984, Bugmann 2001, Shugart 2002). These models simulate the dynamics of a forest by following the fate of individual trees in a stand. Huston and Smith (1987) have shown that by using the individualistic approach of gap models a complex variety of successional patterns can be predicted. These models have been used primarily to predict changes in community structure over time and to assess the effects of climate change on forest structure. Only a few gap models have been hybridized with ecosystem models to study changes in biogeochemical cycles (e.g., LINKAGES: Post and Pastor 1996, HYBRID: Friend et al. 1997, STANDCARB: Harmon and Domingo 2001). With this type of hybrid model it is possible to study the effects of community dynamics on the overall carbon cycle because species replacement is modeled explicitly and fluxes of carbon fixation and respiration can be predicted.

Population and community dynamics occur at an intermediate level between physiology and ecosystem processes but are often ignored in ecosystem models. When excluding population and community dynamics in ecosystem models, several possible assumptions are tacitly made. For population dynamics it is assumed that: colonization lags are minimal, and/or variability introduced by variation in mortality completely dampens as temporal and spatial extent increases. For community dynamics it is assumed that either: 1) species are all similar in terms of ecosystem function, or 2) species have different traits relevant to ecosystem function, but the mixture of species never changes, or 3) the

mixture of species is changing but their effect on ecosystem function is not large enough to matter. A large body of literature provides evidence to reject assumptions 1 and 2 (e.g., Tilman 1985, Huston and Smith 1987, Wedin and Tilman 1990, Huston and Gilbert 1996, Hooper and Vitousek 1997, Chapin et al. 2000, Guariguata and Ostertag 2001, Loreau et al. 2001, Tilman et al. 2001, Franklin et al. 2002). Assumption 3 is a matter of the desired resolution of answers, but arbitrary unless quantified.

Here we present an analysis of population and community processes that may influence dynamics at the ecosystem level and therefore may be relevant to modeling carbon dynamics. We used information from a tropical forest in Colombia as an example test case. Our main research question was: What behaviors emerge by introducing population and community processes in carbon cycle models? For this analysis we used STANDCARB (Harmon and Domingo 2001), a hybrid model with features of gap and ecosystem models.

Methods

Description of the model

STANDCARB is a simulation model of living and dead C pools of forest stands. It had been used to simulate the effects of land cover change, rotation length, tree utilization level, and forest management on C stores in the Pacific Northwest of the US (Harmon and Marks 2002). It was also used to simulate the effects of light limitations and wind mortality on C stocks (Smithwick et al. 2003), and estimate C fluxes in the Pacific Northwest (Cohen et al. 1996). With this model it is possible to examine the effects that

climate, tree species, succession, wildfire, timber harvest, site preparation, and regeneration have on carbon dynamics. Calculations are made over a grid of cells to simulate interactions between trees such as competition for light. Each cell can be colonized by 4 different layers of plants: herbs, shrubs, lower trees, and upper trees. The former represents advanced regeneration and the latter dominant trees. Live pools are divided in seven parts within each layer and six dead pools are derived from the live parts (Figure 4.1). Dead pools in turn form three stable pools derived from decomposing foliage, wood, or belowground parts. Forest processes are simulated through 12 major modules (Table 4.1). The model outputs total live biomass for individual populations and the community, as well as total carbon stocks for the stand.

Parameterization

Parameters to run STANDCARB were selected to predict carbon stores measured in mature tropical forests of the Porce region of Colombia as reported in Chapter 2. These parameters values were obtained through a literature review and from independent information available for the study site.

Five functional types of trees were simulated in this study: early successional, late successional, legumes, palms, and gap species. The rationale for the selection of these groups was that each group has different traits associated with different ecosystem processes relevant to carbon dynamics (Table 4.2). The parameters for each group are presented in Table 4.3.

Simulations

1. Population processes

A set of simulations were designed to look at the effects of colonization and mortality rates on total live biomass. A sensitivity analysis was performed at different values of the colonization and mortality rates. Rates of colonization used were 1.0, 0.5, 0.1, 0.05, and 0.01 per year; which corresponds to a range of colonization of one to 300 years. Mortality rates were 0.01, 0.02, 0.04, and 0.06 per year; which corresponds to a maximum range in life-span of 50 to 300 years. Either an early or a late successional species were used in each simulation (Table 4.3). For the late successional species we assumed that it can regenerate under itself as well as under high light levels. We made this change because using the actual parameters for regeneration (Table 4.3) the population would never establish on its own.

Two different types of mortality rates were evaluated. In a first set of tests, mortality was simulated as a constant rate for each year which assumed that the population can immediately replace live carbon that was lost. In the second set of tests, mortality was simulated as a variable stochastic process which averaged the constant mortality rate, but varied to acknowledge that this process varies spatially and temporally.

The degree of variation introduced by spatial variability in mortality is likely influenced by the relative size of the cells to the stands' extent (Turner et al. 1993). We therefore tested the effect of the spatial extent simulated on the degree of variation that can be obtained for total biomass of each population. Simulations for the early and late

successional species were performed at grid sizes of 7x7, 10x10, 15x15, 20x20, and 25x25 cells. Variation was assessed using the coefficient of variation of the average live biomass for the last 800 years of the simulations. For the early successional species we also calculated the long-term variation using a 10-year window to filter out the short-term variation. We also used a spectral density graph to visually assess changes in variance when the behavior of live biomass was oscillatory (Shugart 1984).

We tested the effect of initial foliage mass on creating lags for regeneration. Ecosystem models can produce lags as a result of the initial foliage mass (or leaf area) assumed that are not associated with population processes. We contrasted the effects of colonization with the effects of ecosystem process on creating lags. We ran simulations with initial foliage mass at values of 0.1, 0.5, 1, 5, and 7 Mg C ha^{-1} assuming a colonization rate of 1.0. The latter foliage mass was close to the maximum that was observed in the simulations and thus represented the case with no lag in foliage mass.

2. Community processes

A set of simulations were performed to analyze the effect of community-related parameters on total live biomass and total carbon stores. In one set of simulations we tested the effects of regeneration-related parameters on the successional behavior of two coexisting species. Specifically, the parameters determining the range of light requirements for regeneration of each species were varied in these set of simulations (Table 4.3). Light requirement for regeneration was partitioned between the two species, allowing each species to regenerate only under a specific range. One of the species was

allowed to regenerate only between 100% available light and an intermediate point which we called the light overlap point (LOP). The other species was allowed to regenerate in a range between the LOP and 20% available light. The analysis was performed for LOPs of 90, 80, 70, and 60% available light. For this set of simulations all parameters were the same for the two species, except for the light requirement range. In another set of simulations, the same analysis was performed but using parameters specific to the early and the late successional species (Table 4.3).

The effect of cell size on light availability for regeneration was studied in a different set of simulations. Interaction between cells causes shading, which depends on the height of trees in neighboring cells. Shading decreases as cell width increases for a given tree height. Simulations at cell widths of 10, 15, 17, 20, and 25 m were performed. Effects of cell width were compared for live biomass and its variability.

3. Ecosystem processes

In these set of tests we evaluated the effect of differences in growth and decomposition parameters for two species that were similar regarding colonization, light requirements, and mortality. First we simulated two species with identical parameters, and then we changed growth- and decomposition-related parameters. For the latter we assigned each species the parameters of growth and decay rates that correspond to the early and late successional species (Table 4.3). The effect of changes in growth and decomposition were evaluated on total live biomass and total carbon stores.

The five groups of species considered in this analysis (Table 4.3) were simulated independently, assuming that each group can regenerate by itself with no limitations of light for regeneration. From this set of simulations it is possible to observe the effect of differences associated with each species group on their maximum amount of carbon accumulation as an effect of their differences in ecosystem-related parameters.

4. Integration of ecosystem-community-population processes

In a first set of simulation experiments examining the interactions of the three levels of processes, we used the results from the ecosystem process tests and introduced changes in light requirements of the two test species, so that community dynamics were incorporated. Then we simulated the two species with differences in their ecosystem-, community-, and population-related parameters to see if a different behavior of carbon accumulation was observed after introducing these processes.

In a second set of simulation experiments, we used the five functional types present in our test-case tropical forest to test for the effects of population and community processes on ecosystem carbon stores. First, we simulated the hypothetical tropical forests having the five groups of species with differences in population and community processes, but not ecosystem processes. Then, we excluded population processes by having the same colonization and mortality rates for all species. Similarly, we excluded community processes by allowing all species regenerate when available light ranged from 100 to 20%. We compared total live biomass, total carbon stores, and net ecosystem production (NEP) from these simulations.

In a third set of experiments we asked whether or not the patterns simulated with five distinct groups of species could be reproduced using a single dominant species parameters or averages of the parameters from all species. To perform this test we compared simulations having multiple species with simulations containing one dominant species or by having one species with the average of the parameters from the multi-species simulation. We performed single-species simulations for the late successional and the legume groups because these are the two species most abundant in our forest.

All simulations were performed for 1000 years using a grid of 20 x 20 cells with a cell width of 17 m, except for those we tested as described above. Each simulation was replicated 5 times and unless stated otherwise the average for each year was reported. We performed all simulations as a secondary succession with no vegetation and slash from previous use and assumed an initial carbon content in soils of 228 Mg C ha^{-1}, which corresponds to measurements in the study site reported in Chapter 2.

Comparisons of model outputs were made on total biomass by species (Mg C ha^{-1}), total live biomass of the community (Mg C ha^{-1}), total carbon stores (live, dead, and stable pools) in the ecosystem (Mg C ha^{-1}), and net ecosystem production NEP (Mg C ha^{-1} yr^{-1}). NEP was calculated as the annual change on carbon stores assuming no leaching, fire, or lateral losses, as these were not explicitly simulated.

Results

Population dynamics

The set of simulations with constant mortality rates (Figures 4.2 and 4.3) showed that changes in colonization rates introduced lags in the accumulation of live carbon. For the early successional species the colonization rates had direct effects on the maximum biomass (steady-state solution) that can be achieved, with a marked decrease as colonization rate dropped below 0.05 per year (Figure 4.2). However, the maximum biomass of the late successional population was not affected by colonization rates (Figure 4.3). Mortality rates also affected the live carbon steady-state solution in the two populations simulated, with a decrease as mortality rate increased.

Addition of variable mortality rates introduced variability in live carbon (Figures 4.4 and 4.5). In addition to causing a temporal lag in live carbon accumulation, colonization rates interacted with mortality to affect the variance of the population dynamics. This was particularly evident when the colonization rate dropped below 0.1 per year. The interaction of the two processes was more pronounced for the early successional species than for the late successional species, causing pronounced cycles. This was probably due to the greater restrictions in its light requirements in the former species which allowed regeneration to interact with colonization rates. It is also clear that variability qualitatively changes the behavior of the late successional species, as colonization rate did limit the steady-state biomass predicted.

We found that the number of cells simulated had an important effect on the short term variability observed in the previous tests. Increases in grid size reduced the inter-annual variability for periods lower than 10 years (Figures 4.6 and 4.7). However, the variation at cycles longer than 10 years observed for both species was not influenced by grid size and does not appear to dampen out as spatial extent increases.

Initial foliage mass influenced lags for the early and late successional species (Figure 4.8). These lags were between 5 and 10 years in a range of foliage mass between 0.1 and 1.0 Mg C ha^{-1}. Lags can be easily observed using the second derivative of the biomass accumulation function (Figure 4.8), as the inflection point of the curve that occurs when the second derivative crosses the x-axes. For values of foliage mass above 5 Mg C ha^{-1} our simulations did not show lags for the two species, suggesting that this amount of foliage can produce nearly the maximum amount of live biomass at these ages. Regeneration lags observed as an effect of colonization rates were usually between 7 and 20 years. Theses results suggest that population processes can introduce regeneration lags in addition to lags associated with low initial foliage mass.

Community processes

The range of available light in which species can regenerate and establish has important effects on the relative abundance of the biomass of each species during a successional sequence (Figure 4.9). The different ranges simulated of light requirements produced different successional behaviors. With a LOP of 0.9 one species dominated initially and then was replaced by the other species as in a classical successional replacement. With a

LOP of 0.8 one species increased and the other decreased producing a divergent behavior, while with a LOP of 0.7 the species biomass tended to become similar in time producing a convergent behavior. With a LOP of 0.6 the total suppression of one of the species was obtained (terminology from Huston and Smith 1987). These behaviors resulted from changes in the light environment over time. Because population- and ecosystem-related parameters of the two species were the same in this set of simulations, total live biomass of the community did not show important differences during the successional sequence (Figure 4.10).

The simulation containing different ecosystem parameters for the early and a late successional species also showed different successional behaviors at difference values of LOPs (Figure 4.11). However, no divergent successional behavior was observed, primarily because the late successional species had higher growth and lower mortality rates, which gave it a competitive advantage relative to the early successional species. Differences in total live biomass, total carbon stores, and net ecosystem production were observed from these simulations using differences in species parameters (Figure 4.12). For example, when LOP was 0.9 there was 50% more live, and 60% more total carbon stores than when LOP was 0.8 or lower. Moreover, when LOP was 0.9 there was a longer period when NEP was positive. However, when LOP was 0.9 there was also an eventual decrease in total carbon stores with NEP being mostly negative once the simulation reached 800 years.

Competition for light is also closely associated with the size of the cells being simulated. We found that as cell width increases total biomass increases and variability associated with competition decreases (Figure 4.13). Given a fixed maximum tree height, as cell width increases the amount of light that can enter a cell increases and the proportion of edge to interior of each cell decreases. This causes competition between cells to decrease which in turn causes live biomass to be higher for each cell. The variation of live biomass over time tends to decrease with increases in cell width (Figure 4.13), which can be explained by the reduction of interactions between cells.

Ecosystem processes

Differences in growth rates between two species led to a 4 fold difference in live biomass compared to a simulation where growth rates were assumed to be identical for the two species and equal to the average growth rate (Figure 4.14). Differences caused by changes in growth rates were also evident in total live biomass and total carbon stores, with the presence of two species with different growth rates causing a faster and ultimately greater store of carbon (Figure 4.15). As expected, differences in decomposition rates between the two species were not associated with differences in total live biomass, but important differences in total carbon stores were observed (Figure 4.16). Specifically, the presence of two species with different decomposition rates lead to a 47% increase in total carbon stores at the steady-state.

Differences in ecosystem parameters of the five groups of species considered in this study resulted in different steady-state solutions for different ecosystem pools (Table

4.4). In this set of simulations the species were simulated independently so the only effects of competition were intra-specific. The largest live biomass was obtained with the group of late successional species as a result of its higher growth rates. However, high growth rates were not necessarily associated with high carbon accumulation in the ecosystem. The largest total carbon stores were observed for the palm group due the effect of the low decomposition rates that causes large accumulation of carbon in the stable pool. The lowest amount of carbon accumulation in the different pools was observed in the dead pool. Decomposition rates were the drivers of carbon accumulation in the dead and stable pools.

Integration of ecosystem-community-population processes

The introduction of differences in light requirements for regeneration in the ecosystem-dynamics simulations generated different patterns of successional replacement depending on the ecosystem parameters changed (Figure 4.17). Differences of decomposition rates between the species did not have an effect on live biomass as growth rates were the same. In contrast, differences in growth rates affected live biomass of the two species because the late successional species had a higher growth rate and subsequently higher biomass. Moreover, the shift in biomass from early to late successional species was earlier when growth rates differed.

The replacement of species with different growth rates generated a temporal pattern that differs from the simulation that assumed no differences in light requirements (Figure 4.18). Because the early successional species had a lower growth rate than the late

successional species, total live biomass and total carbon stores were lower during the first stages of succession and became greater in later stages than the case when there was no differences in light requirements. The same pattern was observed in total carbon stores for the interaction between light requirements and decomposition rates (Figure 4.19), which caused a small but noticeable secondary increase in NEP from 300 to 700 years in the simulation.

Introducing to the previous simulation an interaction between the different community- and population-related parameters showed important effects on temporal patterns of total live biomass and total carbon stores accumulation (Figure 4.20). The effects of these interactions were more pronounced for total carbon stores because the effect of differing decomposition rates. As shown in the previous set of simulations, decomposition rates had no effect on total live biomass, but had an important effect on total carbon stores. For this reason there were not significant differences in live biomass between the simulation containing different light and growth parameters than with the simulation containing different light, growth, and decomposition parameters. However, the simulations with an interaction of decomposition and growth rates showed that growth rates can limit the amount of C that can be transferred to the dead pools and thus limit the amount of organic matter that can be accumulated, with a 27% reduction in total carbon stores when this interaction was present (Figure 4.21). The introduction of mortality rates affected the live pools by limiting the biomass that can be attained, reducing it 7%, but had little effect on total carbon stores because its primary effect is to transfers C from the live pools to the dead pools.

Simulations of a hypothetical tropical forest with five species groups showed that the exclusion of population and community processes led to different combinations of species biomass (Figure 4.21). Exclusion of mortality rate differences in populations increased the competitive abilities of the gap group increasing its lifespan and giving it a competitive advantage over the legume successional group. The similarity of light requirements in the no-community simulation gave a competitive advantage to the palms group, which has high potential for biomass accumulation over all groups except late successional species; however, when actual light requirements are added the regeneration of palms and their abundance is limited. Although no important differences were observed in total live biomass for this set of simulation experiments, differences in total carbon stores were observed with the simulations including different population and community parameters being bracketed by those without differences in those parameters (Figure 4.22). These differences are mainly associated with differences in decomposition rates of the species simulated. For example, the increase in the abundance of palms in the simulation with similar light requirements was associated with an increase in total carbon stores due to the low decomposition rates of this group. Conversely, the increase in gap species when mortality rates were similar among species led to higher decomposition rates and a decrease in total carbon stores.

Single-species simulations using the more abundant species from a five-species simulation, did not match the behavior of total live biomass and total carbon stores of the multi-species simulation (Figures 4.23 and 4.24). Nor did the results obtained with a

single-species simulation using the average parameter value of the five-species simulation match the multi-species simulation. None of these simulations were able to adequately represent the behavior produced by multiple species interacting with each other. The simulation using parameters for the late successional species showed the largest values of total live biomass and total carbon stores, as a consequence of its higher growth and slower decomposition rates. In contrast, the simulation with the parameters for the legume species showed a declining pattern of carbon stores over time as a consequence of its higher than average decomposition rates. The simulation with the average of the parameters showed 20% lower total live biomass and 10% lower total carbon stores than the simulation having the 5 species. Differences in the rates of accumulation of total biomass and total carbon stores between simulations can be easily seen in relative terms (Figures 4.23 and 4.24), specially for the initial stages of succession.

Discussion

We used a simulation model to examine how population (colonization and mortality) and community processes (succession of species as controlled by light) potentially influenced carbon stores of a hypothetical tropical forest. It was but one model and one example; however, we believe that the results may be quite general, although they certainly need to be examined in other forests and with other models. Our model did not have nutrient cycling explicitly addressed. So our conclusions are only valid for systems in which nutrients are not in short supply or their availability is greatly changing over time. Therefore, this analysis most likely pertains to secondary succession with moderate

disturbances (no great level of erosion or extreme burning of slash, etc). While exclusion of this facet of ecosystems did restrict the types of behavior at ecosystem level we obtained, they would probably not eliminate the population and community effects observed.

Effects of population processes

1. Colonization rates and lags

In our simulations we found that lags were an important consequence of including population processes. Lags are introduced by several levels of controls. The arrival of propagules, the presence of remnant trees, or the presence of suitable sites can influence the rate that C accumulates during early stages of succession (Brown and Lugo 1990, Turner et al. 1998, Hughes et al. 1999, Guariguata and Ostertag 2001, Mesquita et al. 2001). When extremely low probabilities of colonization or low availability of suitable microsites for regeneration occur the steady-state store can be limited (Figures 4.2 through 4.5). Lags in the development of succession have been observed in tropical forests of Mexico as an effect of the duration of previous land use (Hughes et al. 1999). Similarly, lags in successional development had been observed in the temperate rain forests of the western Cascade mountains in comparison to similar forests in the Coast range in Oregon, USA (Yang et al. 2005).

Similarly, there is also a lag in reaching the “steady-state” C store. That is known to be related to the rate-constants of the processes controlling losses from the various pools (Olson 1963). This is an ecosystem-related control. In our examples, it took between 60

and 120 years to reach the steady-state, depending on the rates simulated. In other systems it might take even longer (Franklin et al. 2002, Janisch and Harmon 2002).

2. Mortality and variability

Our simulations showed that mortality is a process that has impacts on processes at the population, community, and ecosystem levels. At the population level, mortality controls the amount of variability when the forest nears the steady-state. Variations in our simulations only emerged after the colonization phase has been completed and the system was approaching its maximum biomass. This behavior was highly dependent on the maximum age that can be reached by each population and is caused by the fact that the number and size of individuals dying varies from year to year. As these individuals can not be replaced immediately or it takes some time to replace them in terms of size, the amount of C stores varies over time, even when forests are old and approximating a steady-state. The degree of variability is controlled by the amount of biomass removed by mortality and the lags in replacing these trees, which is an interaction between mortality and colonization rates (Figures 4.4 and 4.5). Loss of tree mass is limited by the maximum size of trees which in turn depends on tree age and reduction of growth by competition. As the extent of a stand increases one would expect this population induced variability to decrease. However, we found that the size of the grid did have an effect on short-term variability but not on the long-term variability observed, at least for species with characteristics similar to the early succession species we examined (Figure 4.6). This implies that the assumption that population effects completely average out for large spatial extents needs to be carefully examined for each case.

At the community level, mortality allows succession to occur. The fact that trees die allows them to be replaced by different species. Light requirements for regeneration will determine the probability that a given species will replace a dead tree from the existing species pool. Depending on the maximum longevity of the species dying-out, the replacement will occur sooner or later in the successional sequence.

At the ecosystem level mortality controls the timing of the C accumulation as well as the amount and distribution of C between live, dead, and soil pools. At the ecosystem level there is a small dampening of this population variation effect on total carbon stores given that higher mortality rates mean less live C but also increases inputs to the dead C pool, and ultimately to soil. Nonetheless, for the scales at which NEP is usually determined, variability in mortality is likely to introduce a substantial amount of year to year variability in NEP that could be confused with a long-term trend if this balance is not measured for multiple years (Figures 4.12 and 4.19). The ecosystem level control of mortality is often not appreciated, but one example in North America indicates it can be quite important. In the Pacific Northwest region of the US, trees live 2-4 times longer than trees in the Northeast region. Although NPP in these two cool temperate environments are relatively similar the biomass is over twice as high in the Pacific Northwest forests, partially as a consequence of this difference in mortality (Waring and Franklin 1979, Loehle 1988, Turner et al. 1995, Brown and Schroeder 1999, Law et al. 2004). Similarly, this effect can occur locally. For example, fragmentation in tropical

forests causes edges and small patches that have been associated with increases in mortality which in turn affects total biomass (Nascimento and Laurance 2004).

Effects of community dynamics

Our results indicate that if all species had similar ecosystem-related parameters, then the order of species abundance would not influence temporal patterns of carbon accumulation (Figure 4.10). They also indicate that if the species abundance did not change over time, the ecosystem-related parameters could be different, and this would not influence temporal patterns of carbon accumulation (Figure 4.15). However, our simulations also showed that when species had different ecosystem-related parameters and species abundance changes, the behavior of total carbon stores was very different and more complex than the two simple assumptions generate (Figures 4.18 through 4.22). There is a wealth of literature that supports that idea that species have differences in ecosystem related parameters, such as growth, mortality, and decomposition rates (e.g. Lieberman et al. 1985, Korning and Baslev 1994, Cornelissen 1996, Chambers et al. 2000, Rees et al. 2001, Prescott et al. 2004). There is also a large body of literature on forest succession and replacement of species over time (e.g. Saldarriaga et al. 1988, Brown and Lugo 1990, Peet 1992, Tilman 1993, Guariguata and Ostertag 2001, Franklin et al. 2002). Therefore the two simple assumptions often tacitly used in ecosystem models are likely not strictly valid given our results or the empirical evidence from other studies.

Interaction among population, community, and ecosystem processes

The simulation experiments that contrasted the simple cases above to the most likely differences in species in terms of timing and ecosystem-related parameters showed that while these simple assumptions predicted the overall trend, the inclusion of species or groups caused different patterns to occur. These patterns are relevant to both the accumulation and the NEP curves (Figures 4.12 and 4.19). This interaction of processes resulted in systematic changes of the status of the ecosystem as C source or sink at long time scales (decadal, centennial). As shown in our different simulations, parameters that control population and community dynamics are responsible for the emergence of these patterns. For this reason single species simulations are unable to represent these kinds of trends since it is assumed that either species are similar and/or that mixtures do not change over time. Assuming that these patters can be observed with field data they might be attributed to an external driver such as climate or atmospheric CO_2 concentrations, when in fact they are cause by population or community processes.

Final remarks

While we have demonstrated that population and community processes have the potential to impact temporal patterns of C accumulation, the inclusion of these processes in C models is not necessarily "mandatory". The effects of population processes, and perhaps community processes, are also dependent on the spatial extent examined. For large spatial extents this variation might be dampened. However, with large spatial extent the variation of population and community parameters is likely increased. It also depends on the resolution to the answer that is desired. It may be that the temporal variability introduced

by population and/or community-related process is not relevant to the question being examined, although both are likely to add uncertainty to the results if ignored. It also may be that the temporal extent desired is shorter than the temporal extent in which the effects are relevant. Also it is clear that, for example, that variability due to mortality is dampened until the initial colonization and growth phase is completed. Therefore, if the interval between disturbances is short, it might be "ignored". Likewise, if the interval is very short the species mixture is unlikely to change a great deal and community processes might be "ignored". However, this does not mean that these processes have no effects; their exclusion places an uncertainty limit on the analysis that is not frequently stated. We think that it is important to consider these effects in ecosystem carbon models or be more explicit about the assumptions being made.

Tables

Table 4.1. Ecosystem processes simulated by the 12 modules of STANDCARB.

Module name	**Process simulated**
PLANT and DIEOUT	Species recruitment, replacement and colonization.
GROWTH	Growth of living plant parts.
MORTALITY	Rate of detritus production.
DECOMPOSE	Net C balance in detritus pools.
SPROUT	Individual regeneration from tree sprout.
NEIGHBOR	Light environment of a cell and the interaction with neighboring cells.
SOIL TEXTURE and CLIMATE	Effects of soil texture, depth, and rockiness on water holding capacity.
HARVEST, BURNKILL, and SITEPREP	Effects of silvicultural treatments, harvest or fire on the living and dead pools.

Table 4.2. Species groups used in the simulations and some relevant characteristics to carbon dynamics.

Group	Characteristics	Effects on C dynamics	Some species common in the study area
Early successional	Can colonize mineral soils, high abundance, high light demanding, short lived and fast growing.	High growth rates and turnover, low litter quality.	*Piper* spp., *Heliocarpus americanus, Myrsine* spp., *Vismia* sp.
Legumes	Often dominant plant family. High N concentration in litter.	High litter production and decomposition rates.	*Enterollobium schomburgkii*, *Inga* spp. *Pithecellobium jupumba, Acacia* sp
Palms	Voluminous, high-fiber litter.	Litter with high lignin content and slow decomposition rates.	*Oenocarpus bataua, Euterpe precatoria, Bactris* sp.
Late successional	Dominant plant form. Shade tolerant, long-lived but may be fast growing.	High litter production. Medium litter quality.	*Cedrela odorota, Cordia bicolor, Xilopia sericea. Alchornea megaphylla, Anacardium excelsum, Nectandra* sp., *Ocotea guianensis, Pachira* sp.
Gap species	Colonize small gaps. Shade intolerants, short lived, fast growing.	High turnover, low quality litter.	*Didymopanax morototoni, Byrsonima arthropoda, Pouruma* sp.

Table 4.3. Parameters used for the five functional groups simulated. All parameters dimensionless, unless units provided.

	Early successional	**Late successional**	**Legumes**	**Palms**	**Gap species**
Recruitment parameters					
Light max	1.00	0.90	1.00	0.80	0.95
Light min	0.90	0.20	0.20	0.20	0.80
WaterPot max (MPascals)	3.50	3.50	3.50	3.00	1.50
WaterPot min (MPascals)	0.05	0.05	0.05	0.05	0.05
Growth parameters					
Light comp point (%)	20	5	15	15	10
Foliage ProdRate Max	1.0	0.8	1.0	0.8	1.0
Mortality					
Mortmax	0.08	0.04	0.08	0.03	0.09
Age max (years)	250	500	300	500	100
Decomposition					
k foliage	0.60	0.40	0.99	0.30	0.99
k fine roots	0.65	0.45	0.99	0.30	0.99
k coarse roots	0.35	0.30	0.70	0.30	0.70
k sapwood	0.40	0.30	0.70	0.25	0.70
k heartwood	0.35	0.28	0.55	0.20	0.55
k branch	0.50	0.40	0.80	0.20	0.80

Table 4.4. Steady-state averages ± standard deviations (last 500 years) for each species simulated separately, assuming that they can regenerate by themselves. No restrictions in light requirements were introduced in the simulations. Units in Mg C ha^{-1}.

Carbon pool	Early successional	Late successional	Legumes	Palms	Gap species
Live	117.7 ± 2.9	201.6 ± 3.6	143.7 ± 2.7	166.6 ± 3.6	128.4 ± 3.5
Dead	8.9 ± 0.7	9.4 ± 1.0	4.7 ± 0.6	12.0 ± 1.0	6.3 ± 0.8
Stable	382.0 ± 20.1	560.5 ± 21.3	200.0 ± 7.5	721.9 ± 10.4	226.9 ± 3.2
Total	508.6 ± 20.0	771.5 ± 21.1	348.5 ± 7.0	900.5 ± 10.2	361.6 ± 4.8

Figures

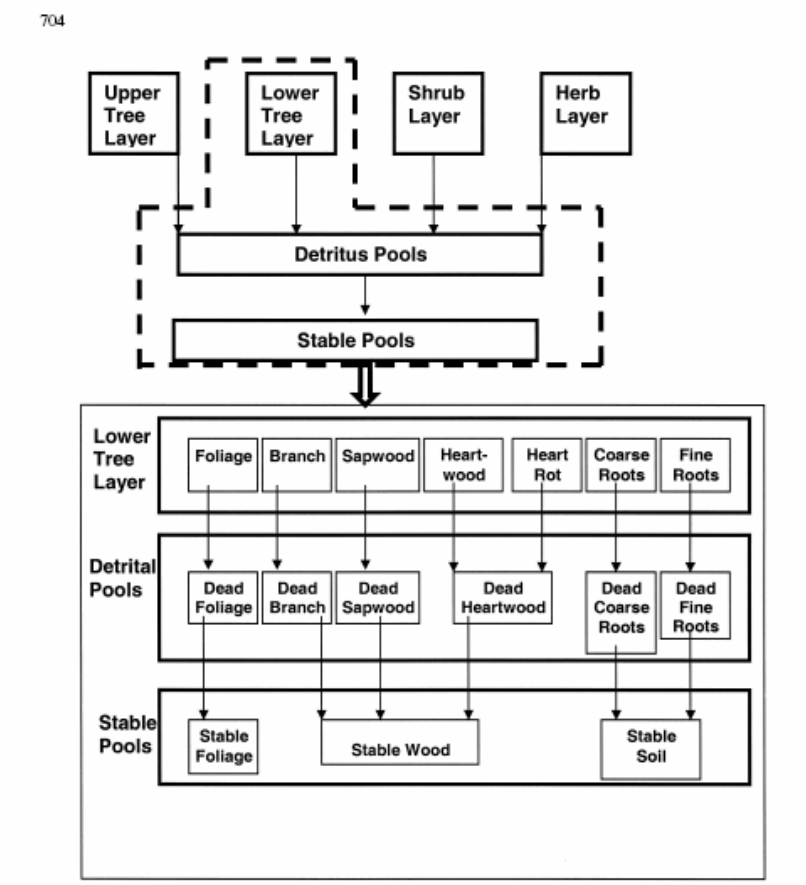

Figure 4.1. Conceptual organization of layers and C pools in STANDCARB 2.0, from (Harmon and Marks 2002).

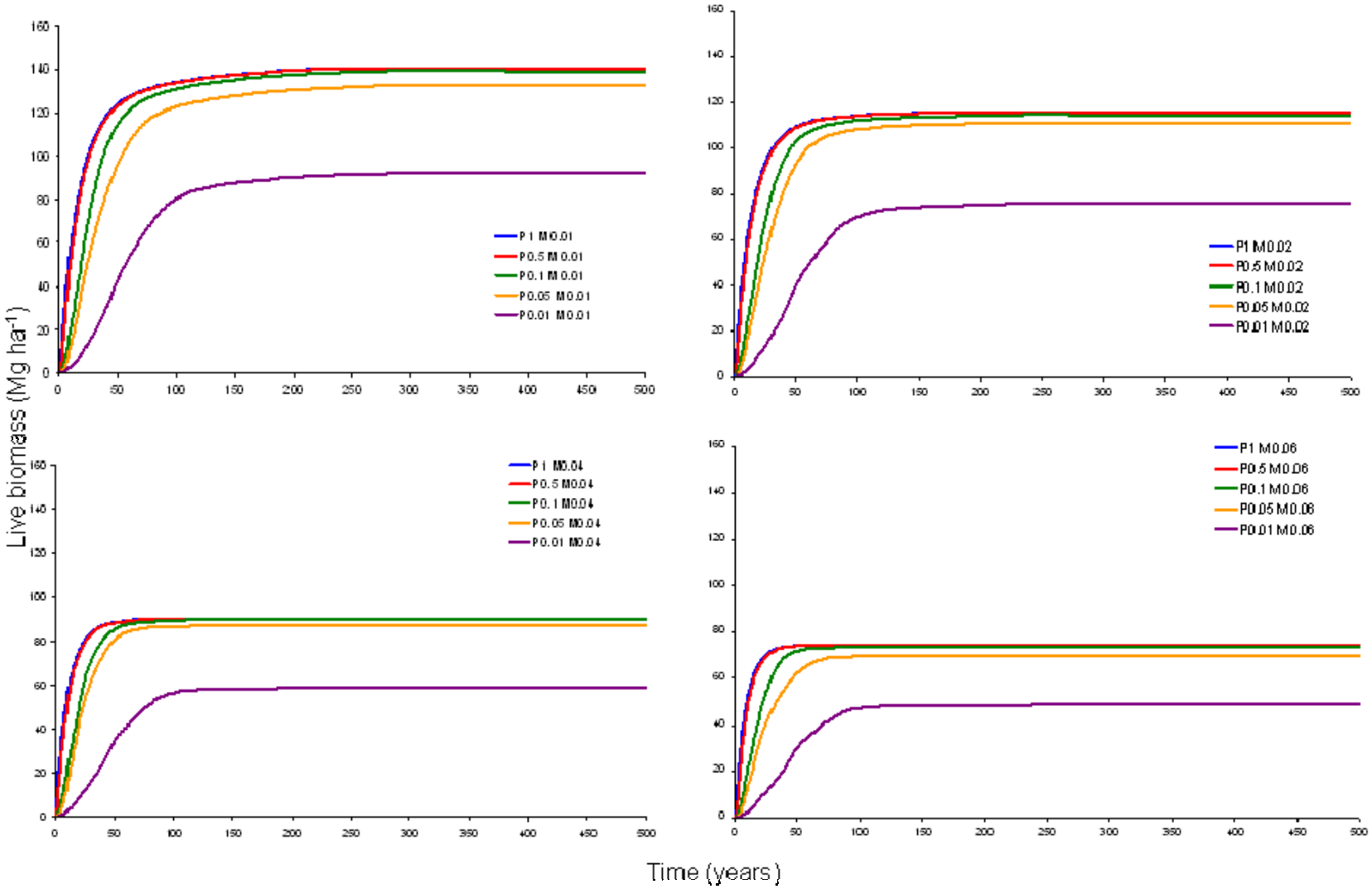

Figure 4.2. Live biomass of an early successional species at different colonization (P) and mortality (M) rates. Each color represents a different simulation. In this set of simulations mortality rates were constant over time.

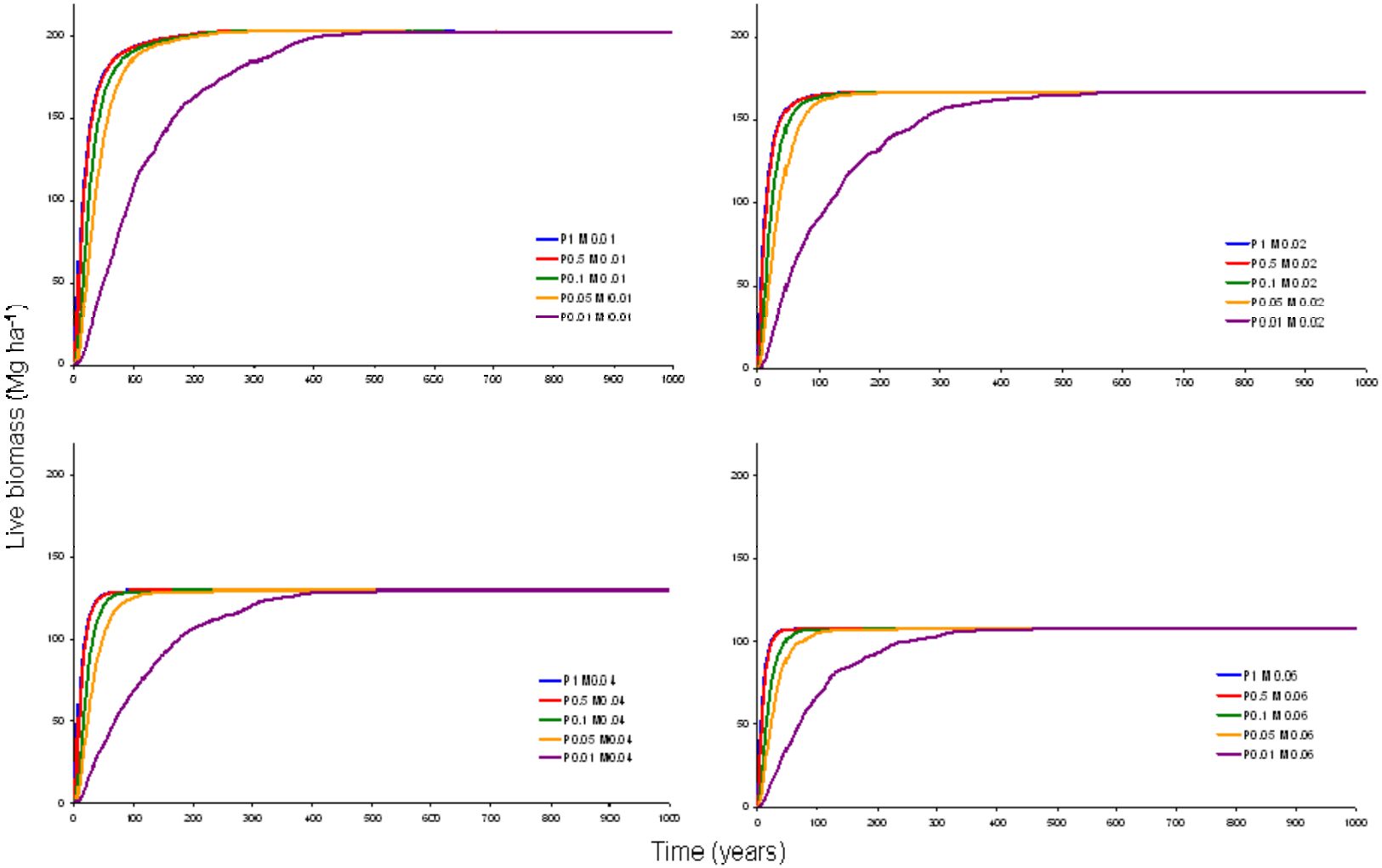

Figure 4.3. Live biomass of a late successional species at different colonization (P) and mortality (M) rates. Each color represents a different simulation. In this set of simulations mortality rates were constant over time.

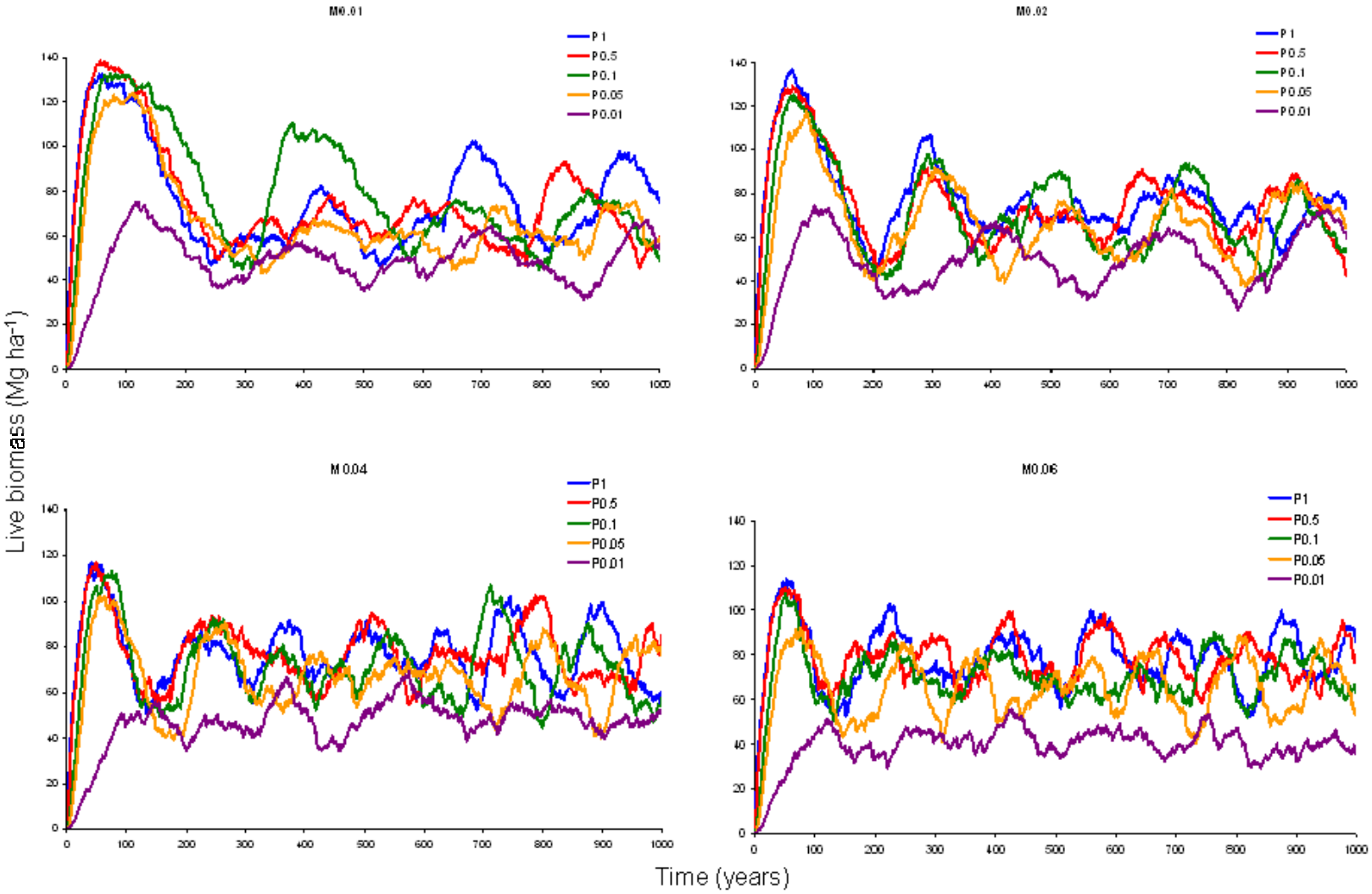

Figure 4.4. Live biomass of an early successional species at different colonization (P) and mortality (M) rates. Each color represents a different simulation. In this set of simulations mortality rates were variable over time but averaged the same as the constant rate used in Figure 4.2.

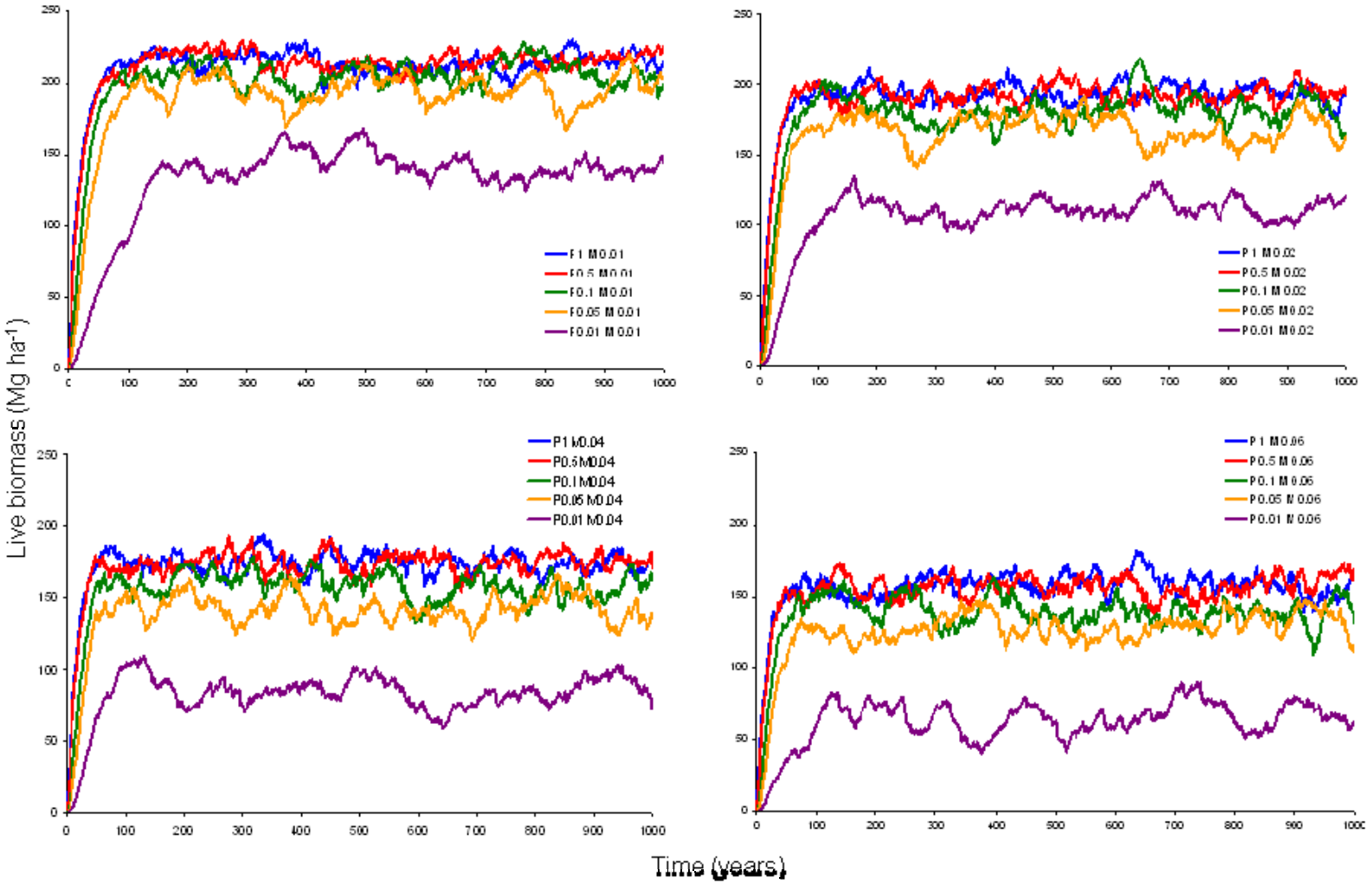

Figure 4.5. Live biomass of a late successional species at different colonization (P) and mortality (M) rates. Each color represents a different simulation. In this set of simulations mortality rates are variable over time averaged the same as the constant rate used in Figure 4.3.

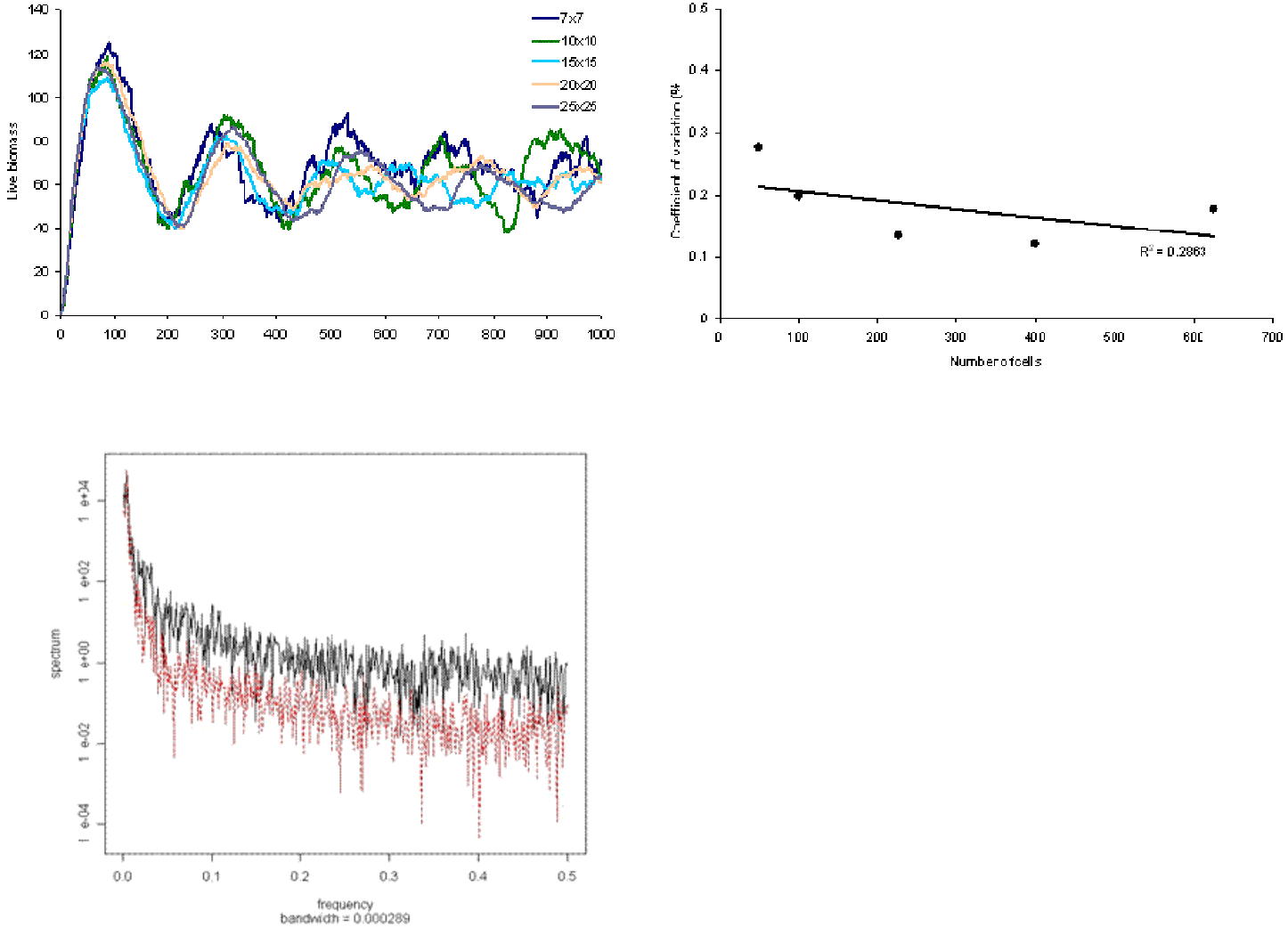

Figure 4.6. Effect of different grid sizes (7x7, 10x10, 15x15, 20x20, and 25x25) on the variability of live biomass for an early successional species with colonization rate of 0.05 and mortality rate of 0.02. The right-upper panel shows the coefficient of variation of live biomass using a filter of 10 years to correct for the long term (>10 years) variability. The lower left panel shows the spectral density for the grid sizes of 7x7 (black line) and 25x25 (red line). In this graph frequency is the inverse of time (years).

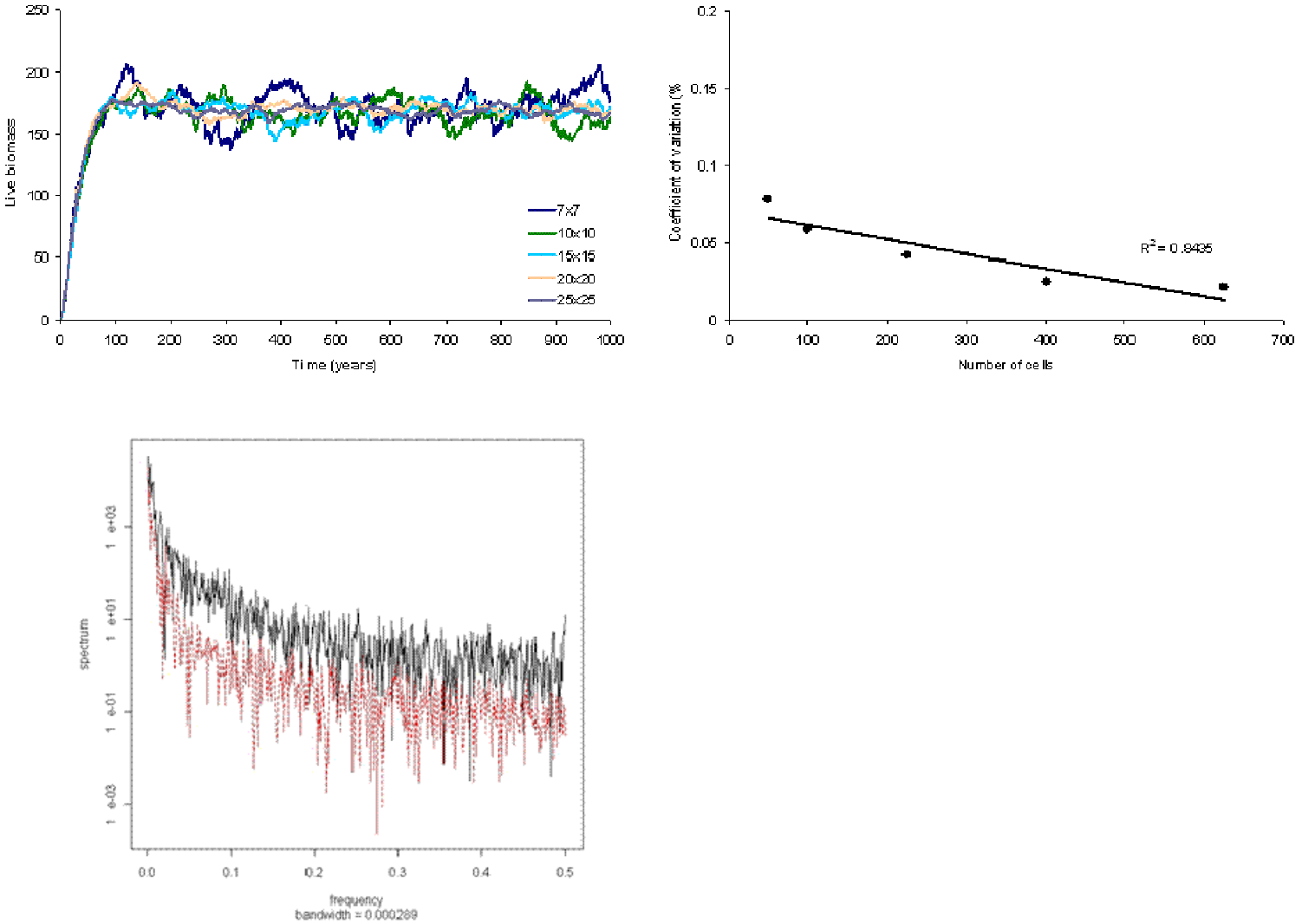

Figure 4.7. Effect of different grid sizes (7x7, 10x10, 15x15, 20x20, and 25x25) on the variability of live biomass for a late successional species with colonization rate of 0.05 and mortality rate of 0.02. The right-upper panel shows the coefficient of variation of live biomass using a filter of 10 years to correct for the long term (>10 years) variability. The lower left panel shows the spectral density for the grid sizes of 7x7 (black line) and 25x25 (red line).

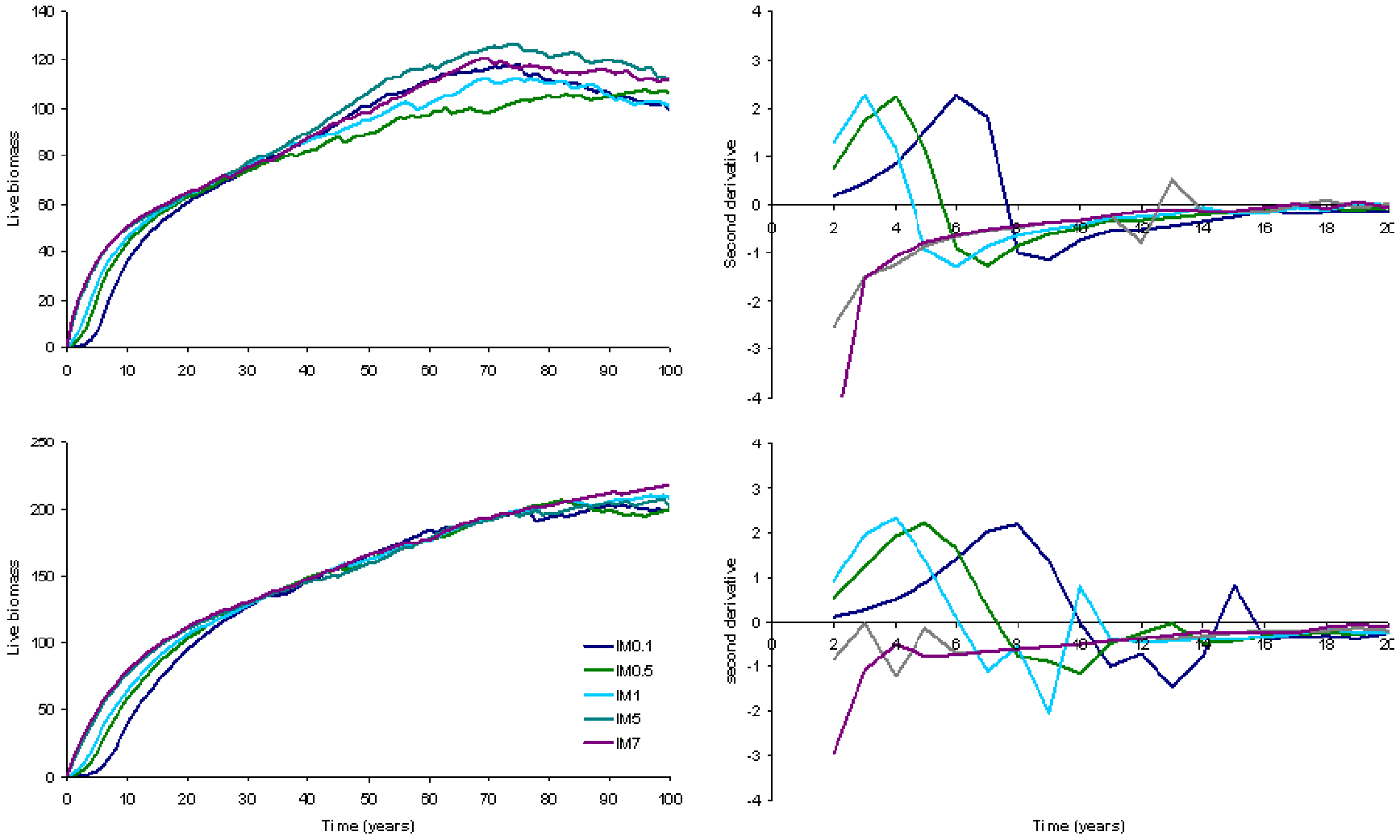

Figure 4.8. Effect of initial foliage mass on live biomass of an early (upper left) and late (lower left) successional species. Simulations for initial foliage mass (IM) of 0.1, 0.5, 1, 5. and 7 Mg C ha^{-1} and colonization rate of 1.0. Second derivatives of the biomass accumulation curves are shown at the right side. The intersection of each line with x-axes denotes the lag for regeneration which corresponds mathematically with the inflection point of the curve.

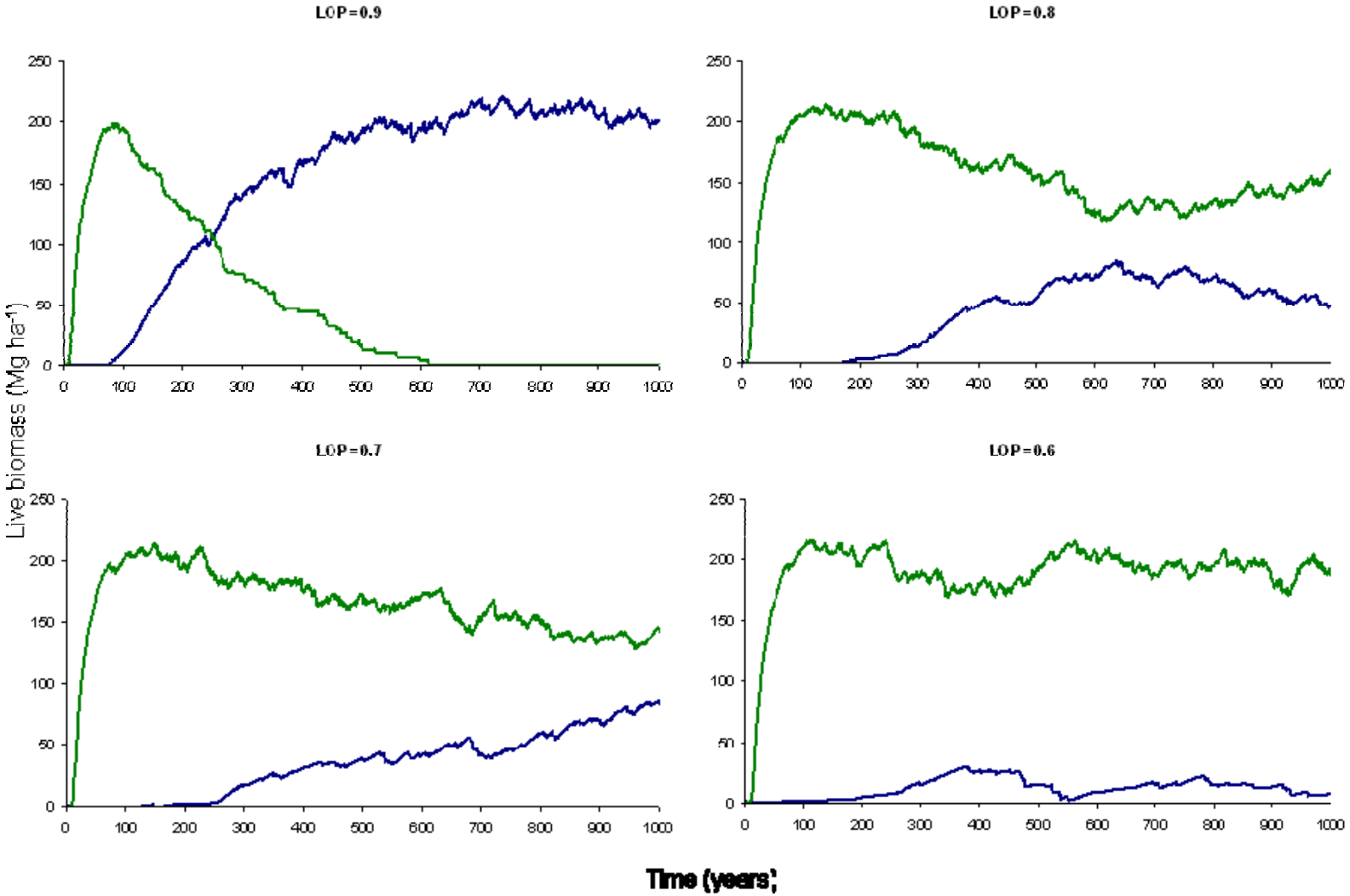

Figure 4.9. Live biomass in simulations with two species at different values of light requirements. Light Overlap Point (LOP) is defined as the case where the light minimum of the early successional species equals the maximum light level of the late successional species.

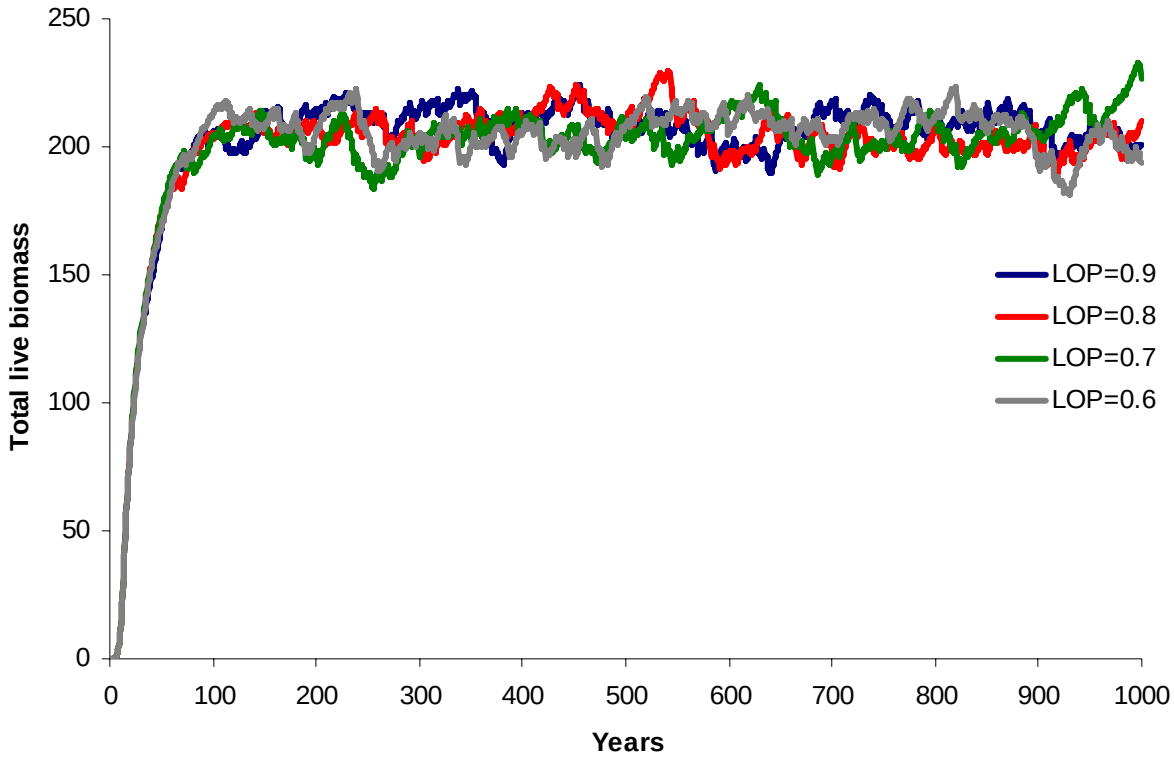

Figure 4.10. Total live biomass in simulations with two similar species at different values of light requirements. Light Overlap Point (LOP) as in Figure 4.9.

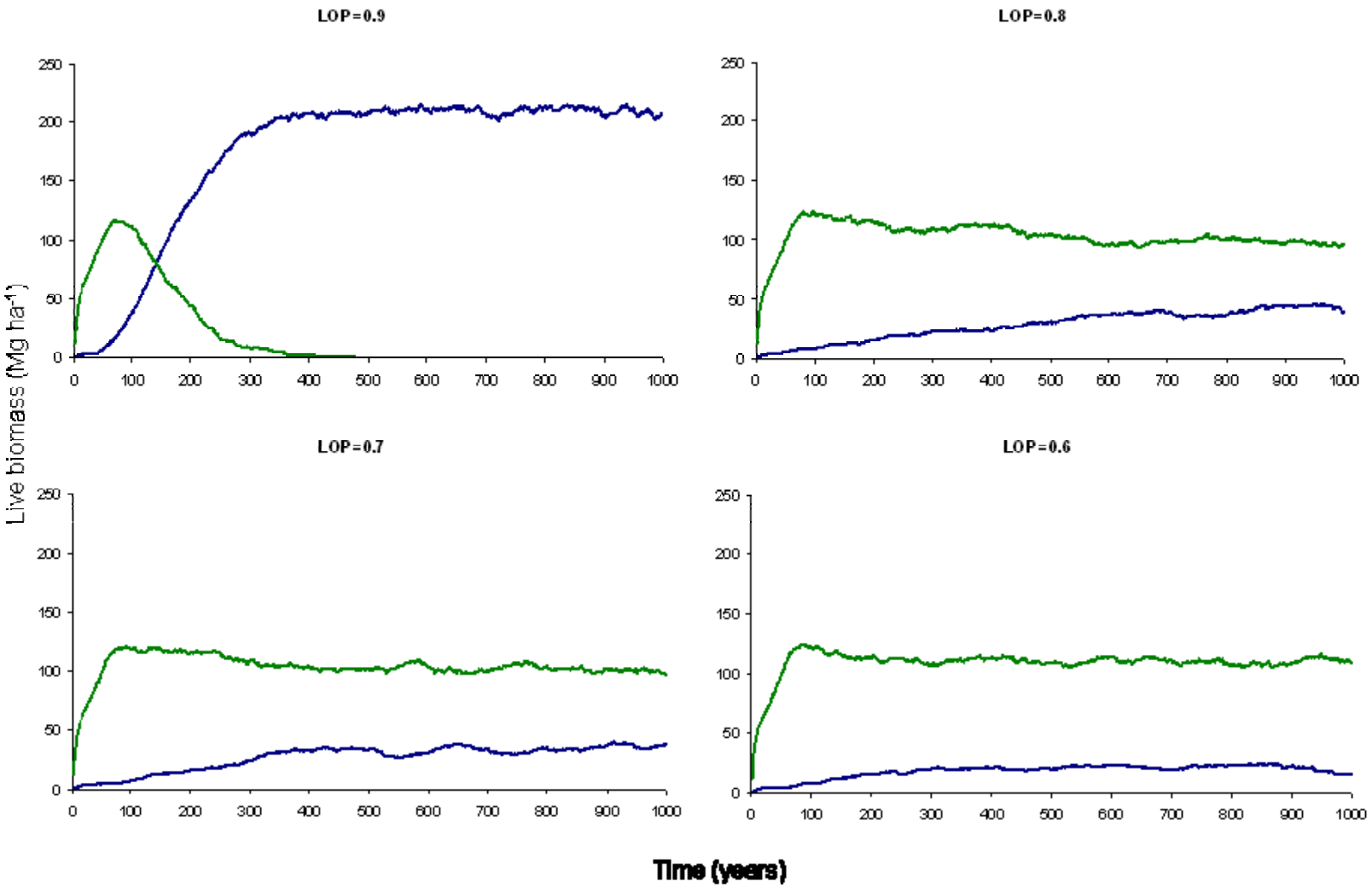

Figure 4.11. Live biomass in simulations with an early and a late successional species at different values of light requirements. Light Overlap Point (LOP) as in Figure 9. All parameters, except light requirements, as in Table 4.3.

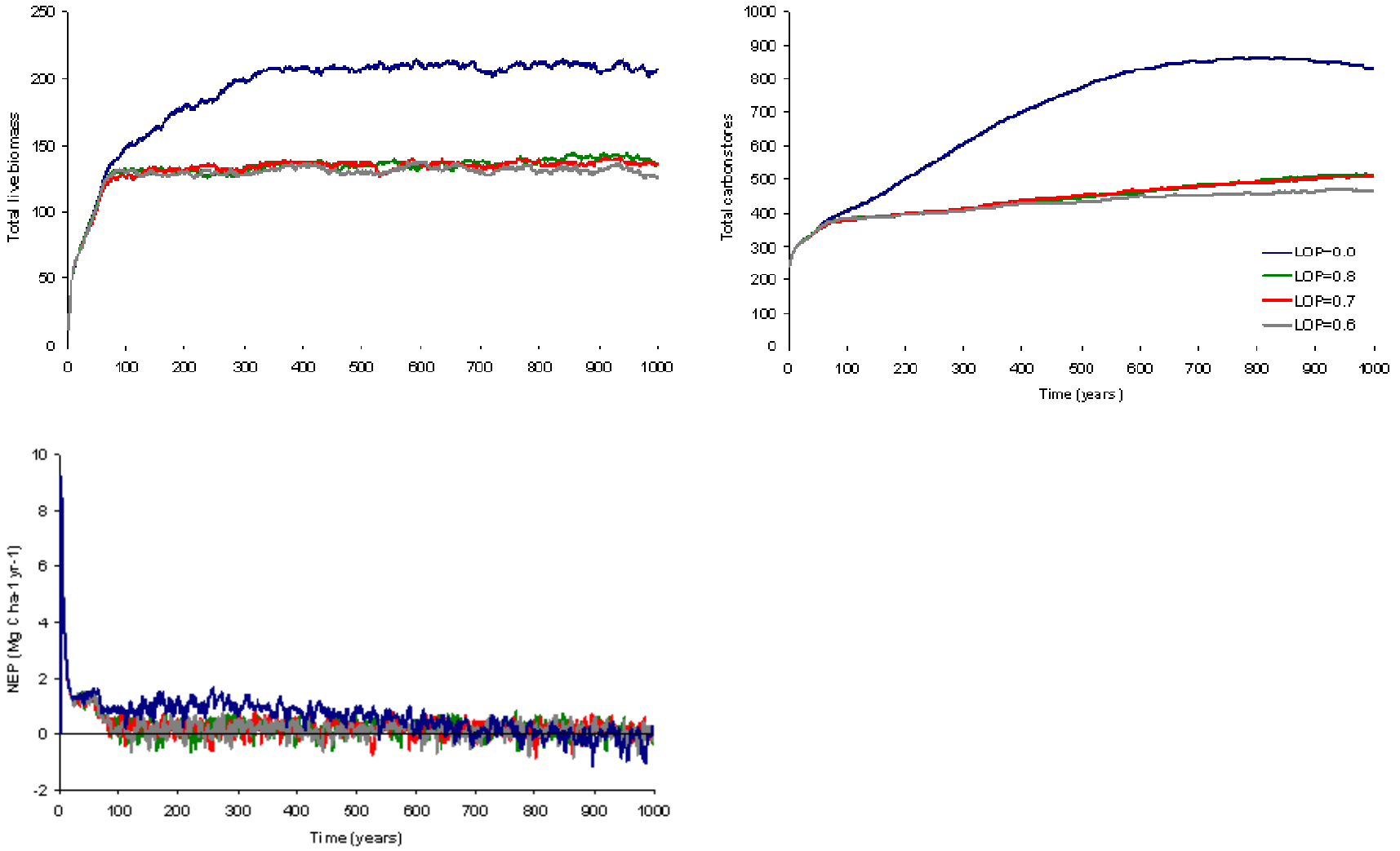

Figure 4.12. Total live biomass, total carbon stores, and net ecosystem production (NEP) in simulations with an early and a late successional species at different values of light requirements. Light Overlap Point (LOP) as in Figure 4.9. All parameters, except light requirements, as in Table 4.3.

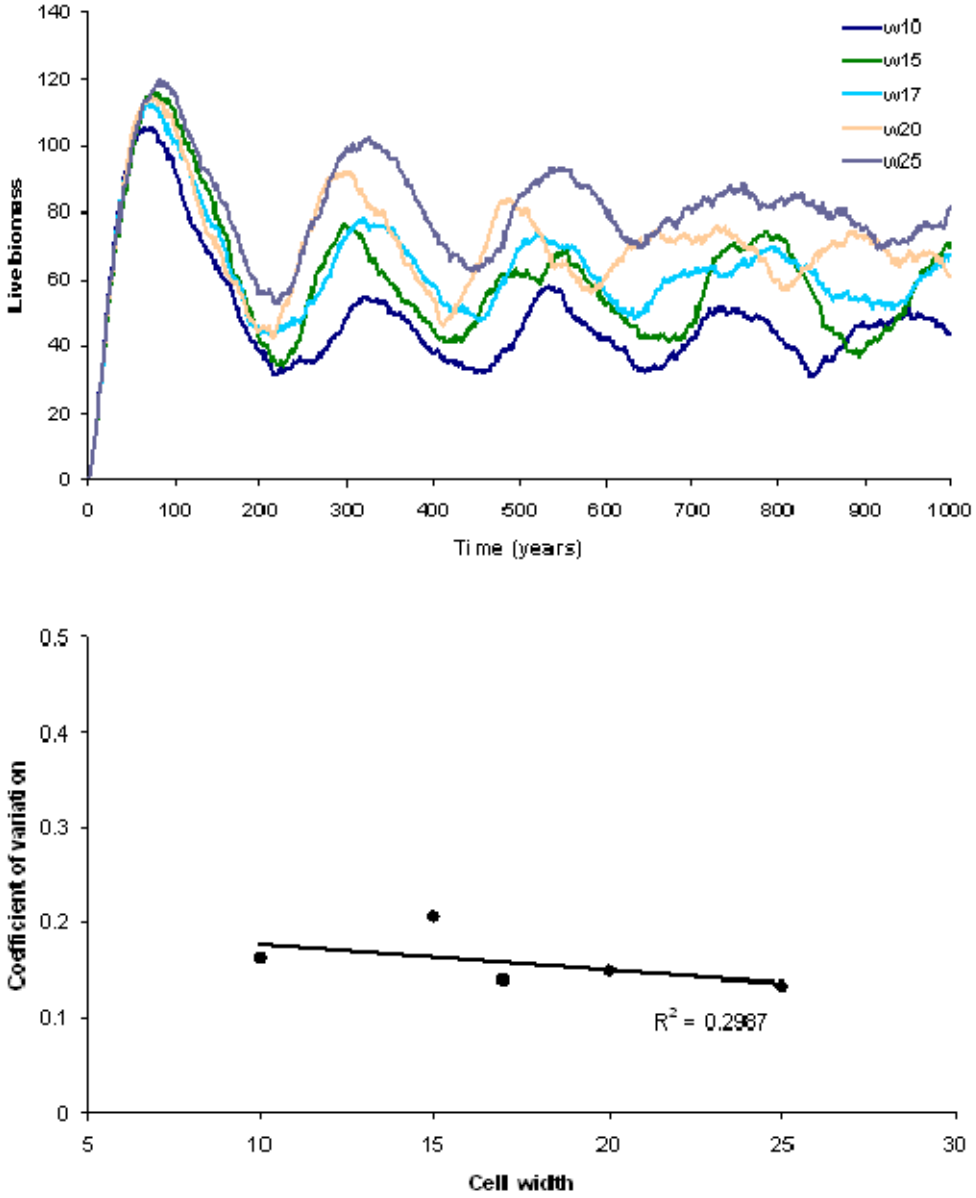

Figure 4.13. Effect of cell width on live biomass (upper panel) of an early successional species with colonization rate of 0.05 and mortality rate 0.02. Lower panel shows the long-term coefficient of variation from the simulations in the upper panel. Simulations with cell widths of 10, 15, 17, 20, and 25 m.

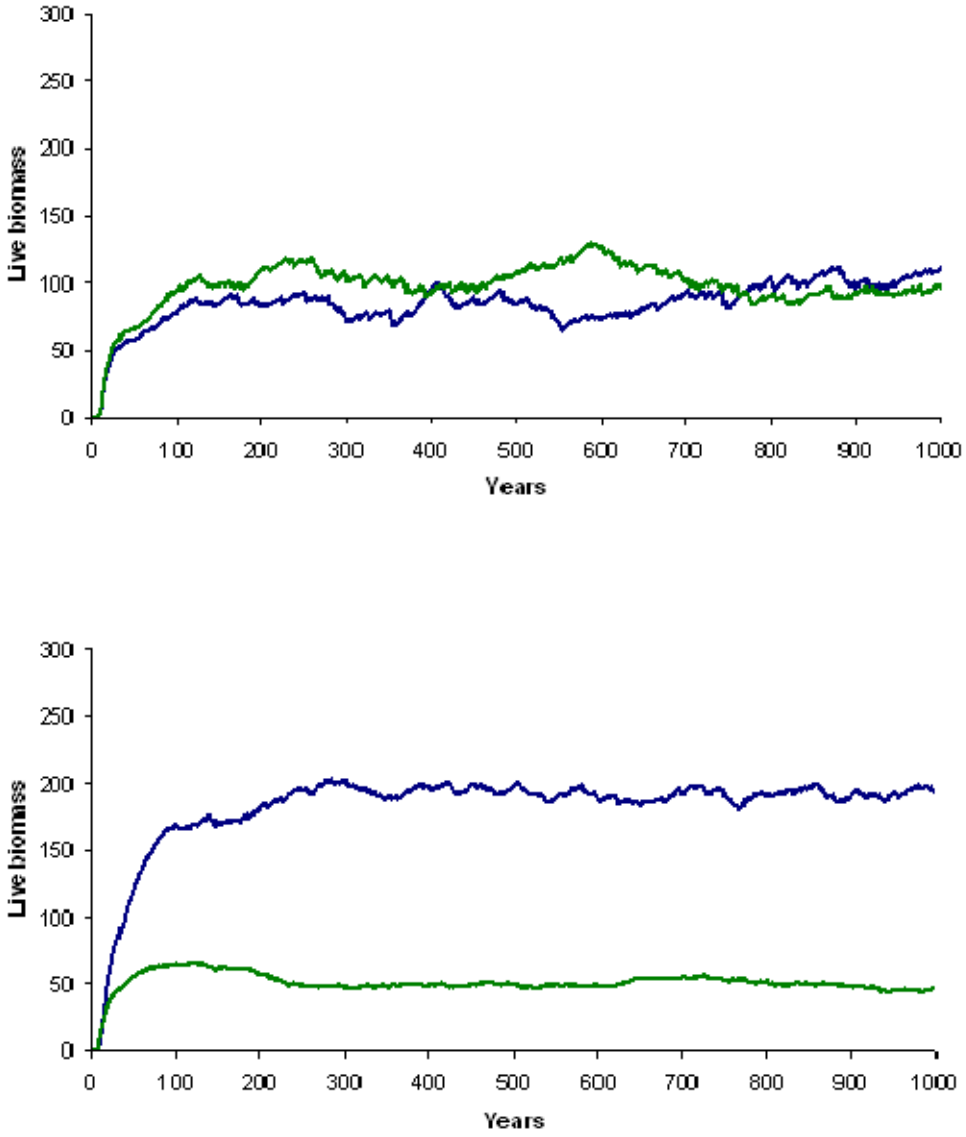

Figure 4.14. Species specific live biomass of two species in two simulations with contrasting assumptions about species differences. The upper panel consists of two similar species with all parameters equal. The lower panel consists of two species with different growth rates. The growth rates used are the rates presented in Table 4.3 for an early and late successional species.

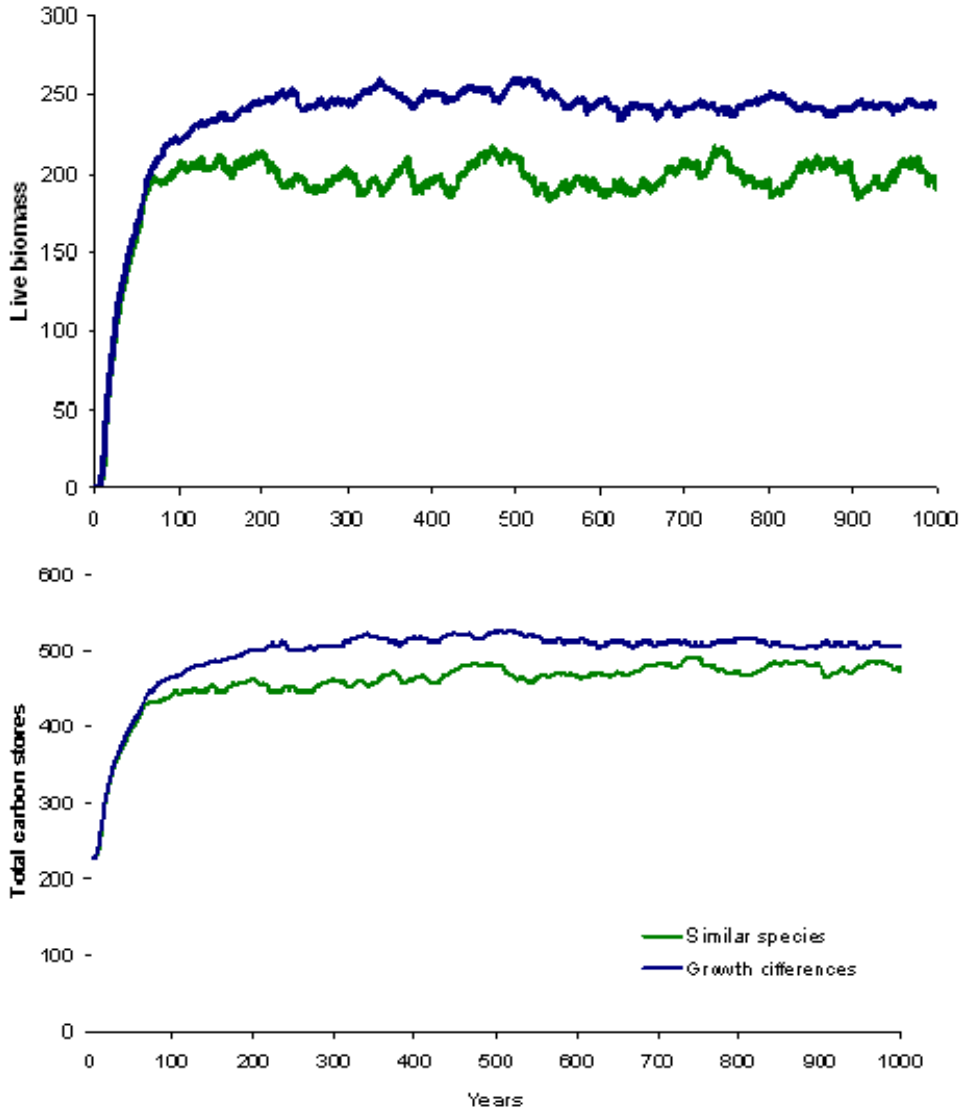

Figure 4.15. Total live biomass and total carbon stores of two species in two different simulations with contrasting assumptions about species differences. One simulation was performed with all parameters equal and the other simulation with only differences in growth rates for the two species. The growth rates used are the rates presented in Table 4.3 for an early and late successional species.

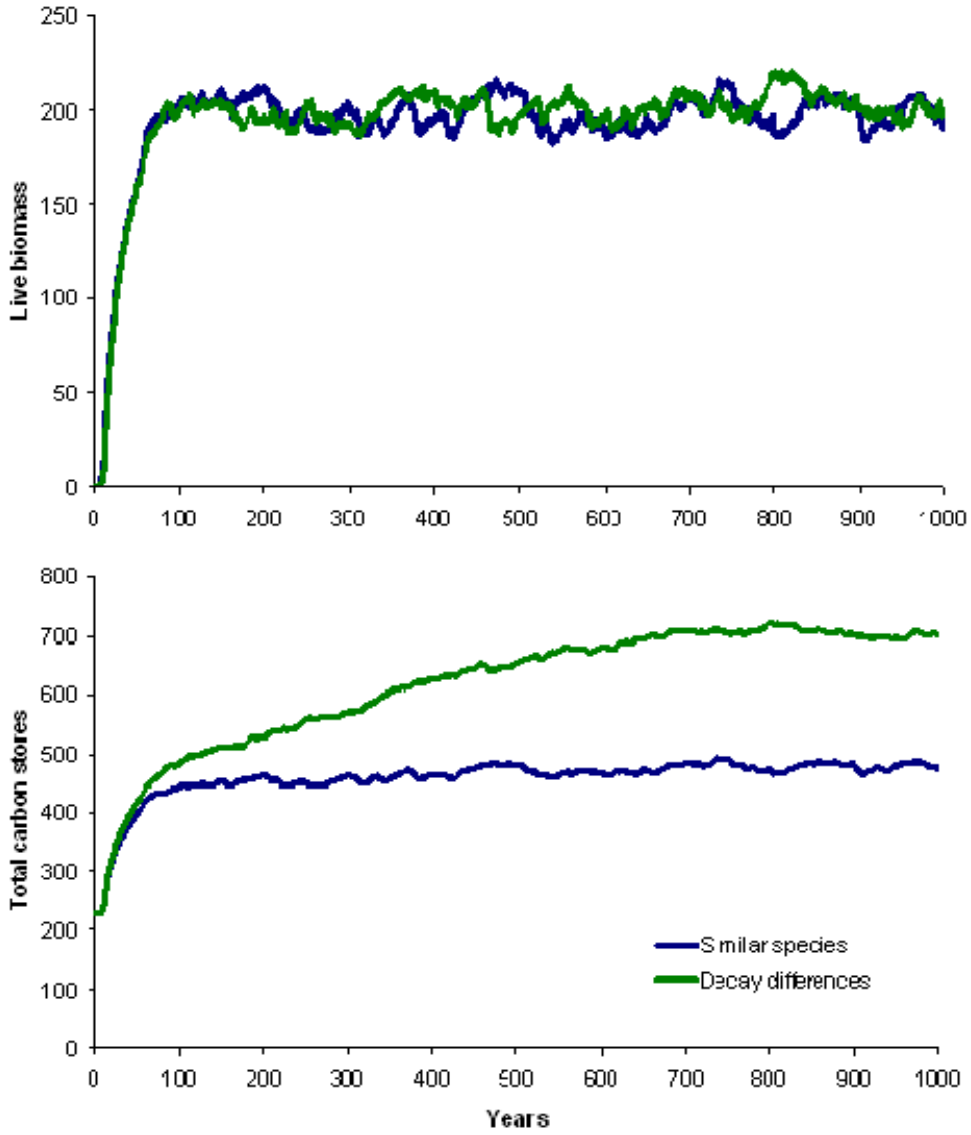

Figure 4.16. Total live biomass and total carbon stores of two species in two different simulations with contrasting assumptions about species differences The brighter line represents a simulation with all parameter equal for the two species and darker line represent the simulation with only differences in decomposition rates for the two species. The decomposition rates used are the rates presented in Table 4.3 for a legume and a palm species.

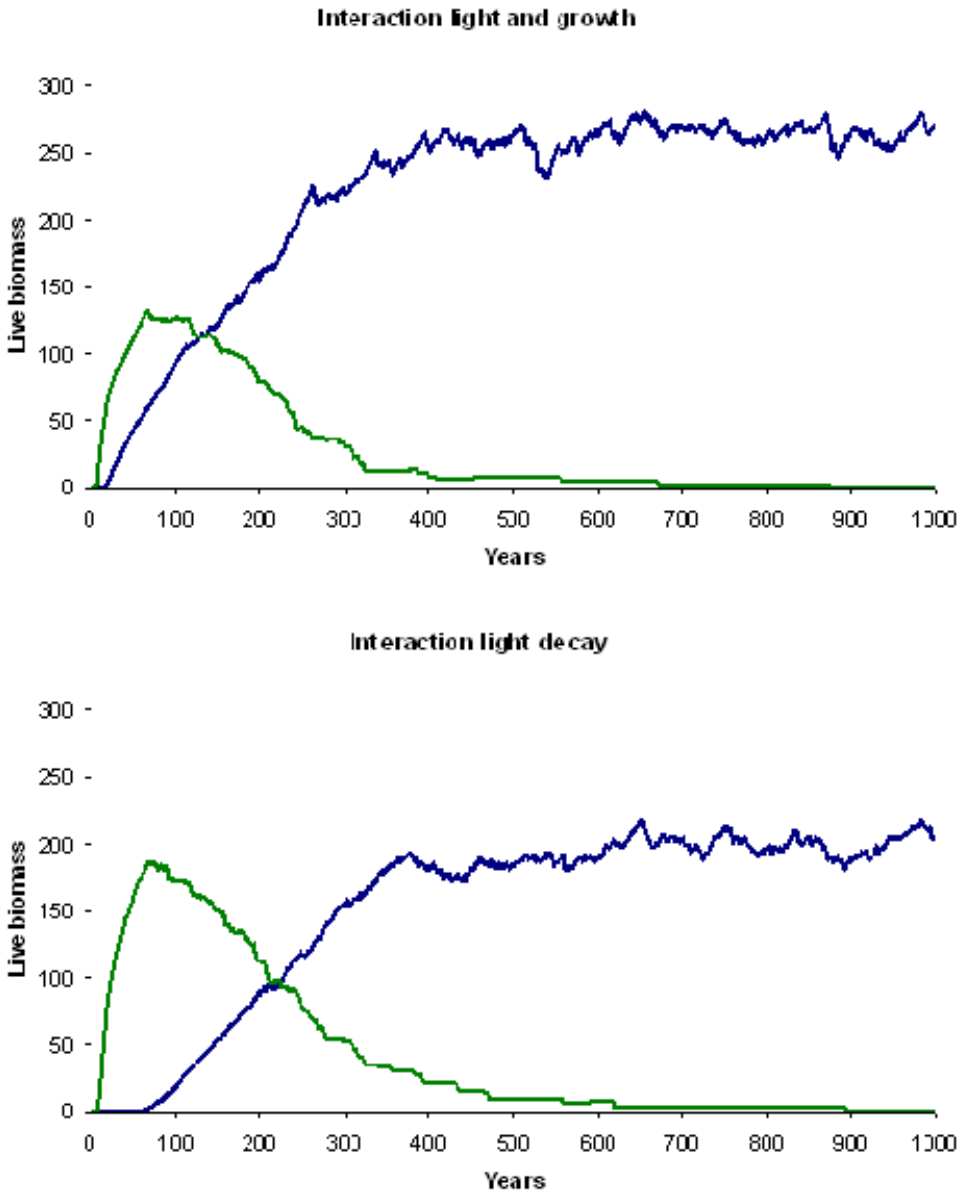

Figure 4.17. Species-specific live carbon stores as a function of the interaction between light requirement parameters with growth (upper panel) and decomposition rates (lower panel).

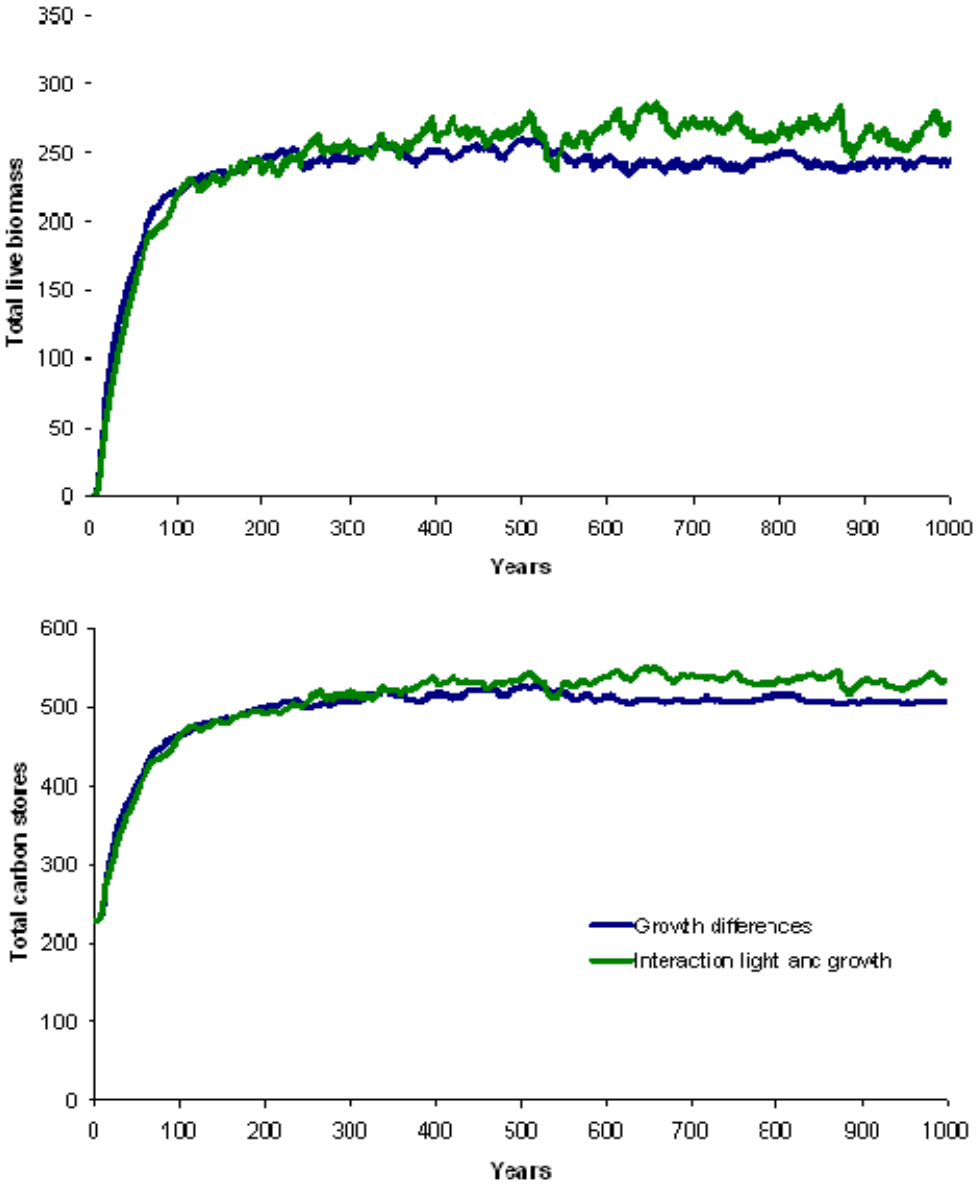

Figure 4.18. Effects of the interaction between light requirement and growth rates on total live biomass (upper panel) and total carbon stores (lower panel).

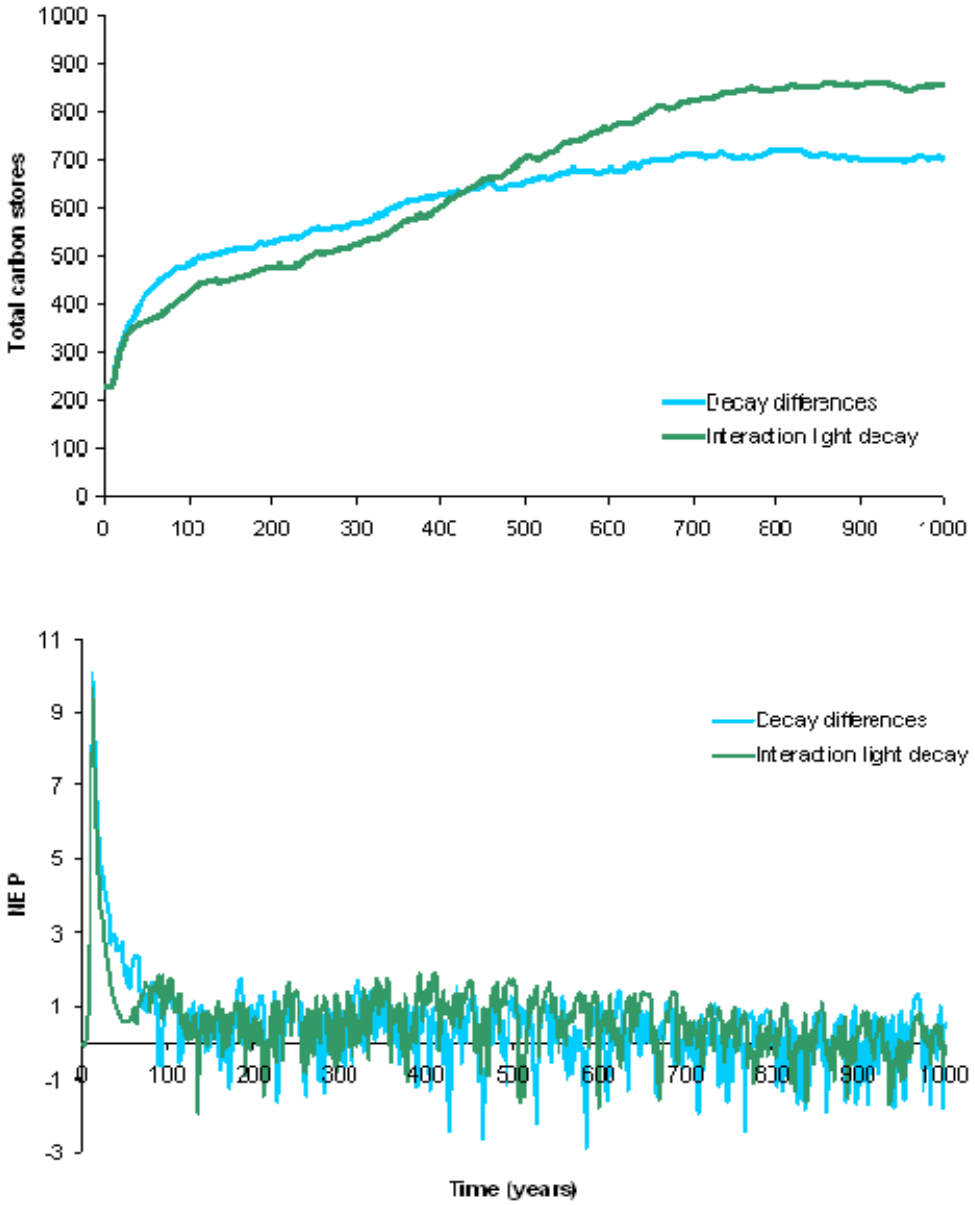

Figure 4.19. Effects of the interaction between light requirements and decomposition rates on total carbon stores (upper panel) and net ecosystem production (lower panel).

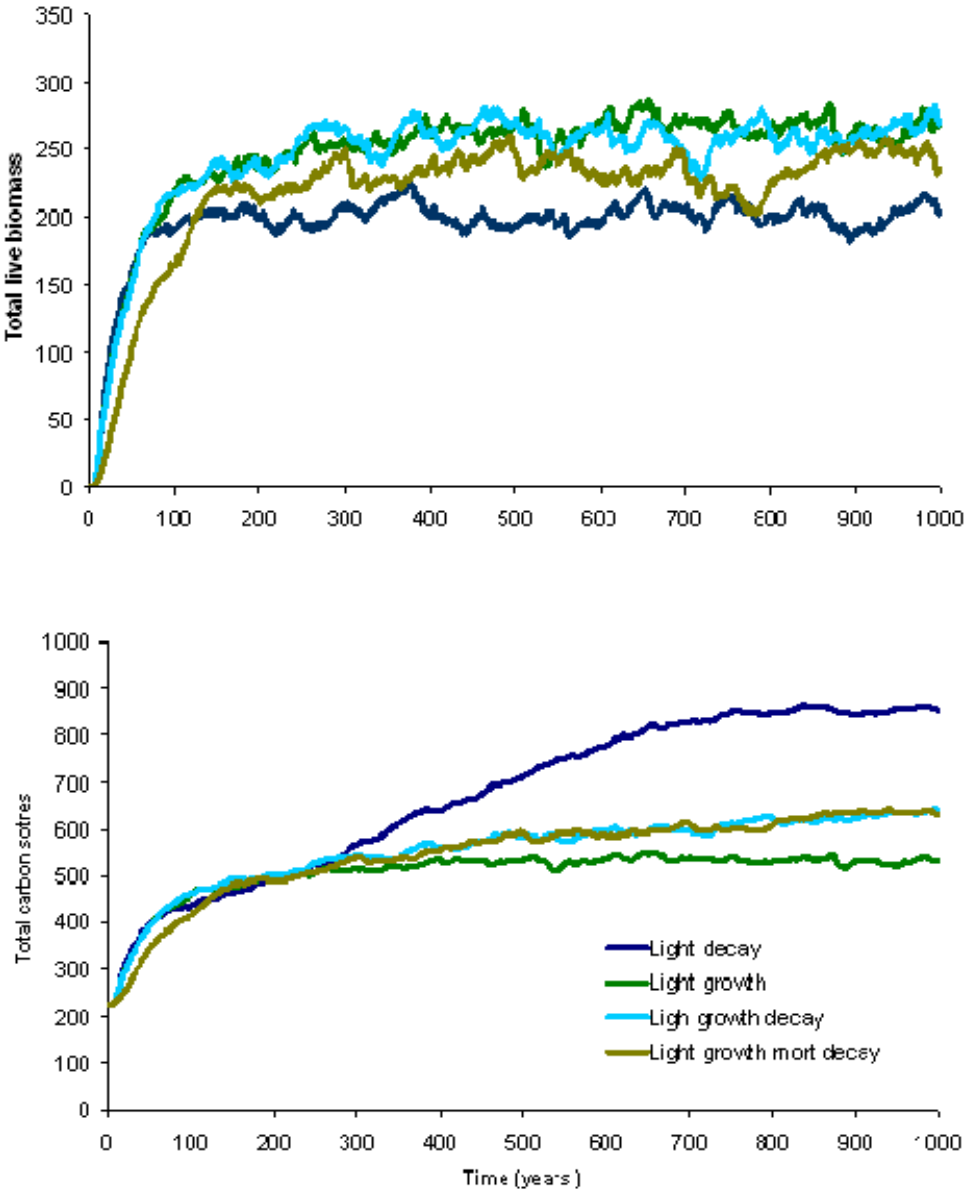

Figure 4.20. Total live biomass (upper) and total carbon stores (lower) of simulations with: different decomposition rates and light requirements (light decay); different growth rates and light requirements (light growth); different rates of growth, decomposition, and light requirements (light growth decay); and different rates of growth, decomposition, mortality, and light requirements (light growth mort decay).

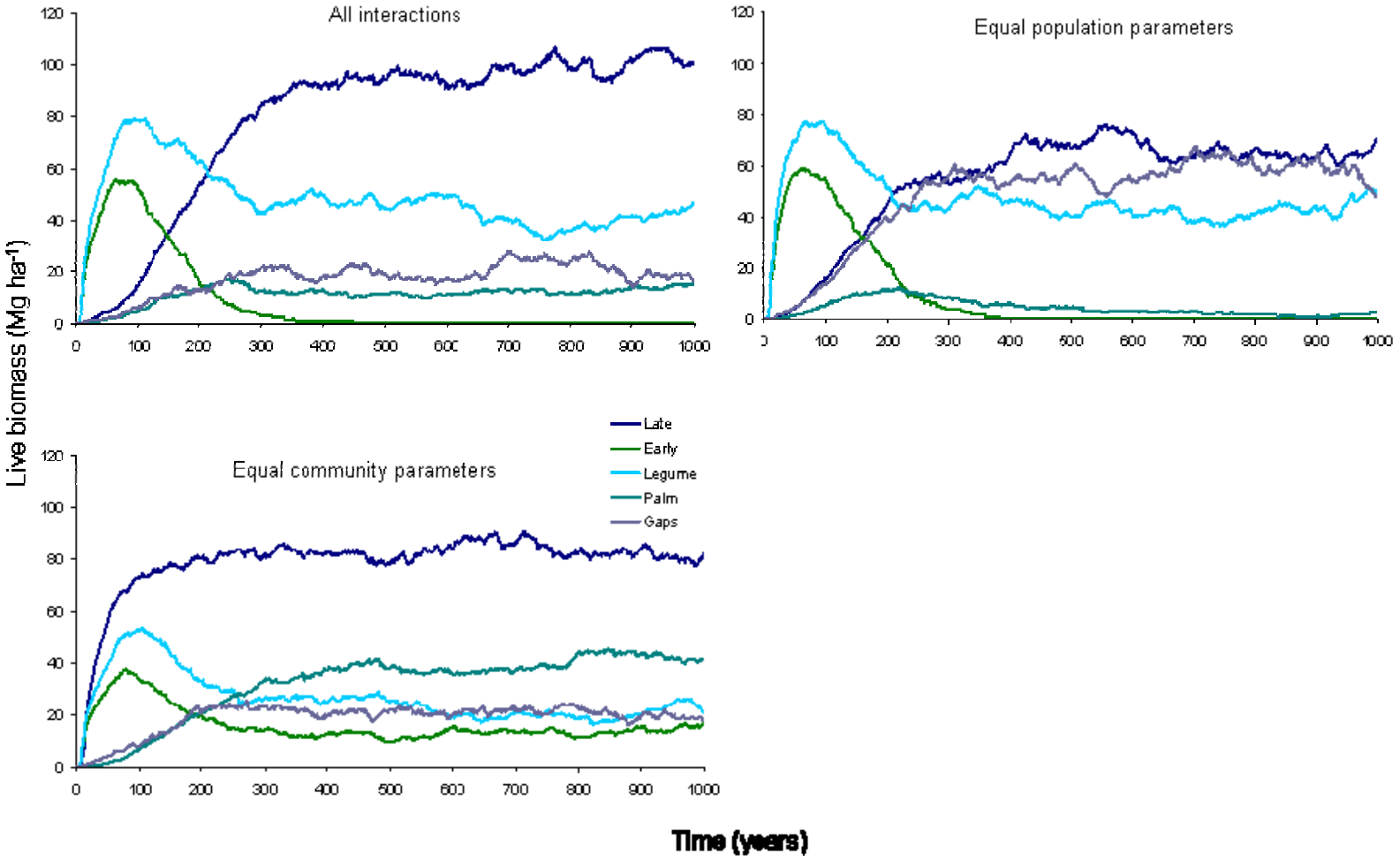

Figure 4.21. Simulation of a hypothetical tropical forest with five different functional groups. Parameters for the five groups are different in the simulation presented in the upper left corner. Population-related parameters, i.e. mortality and colonization rates, were similar for the simulation in the upper right corner. Community-related parameters, i.e. light requierements, were all the same for the simulation in the lower left corner.

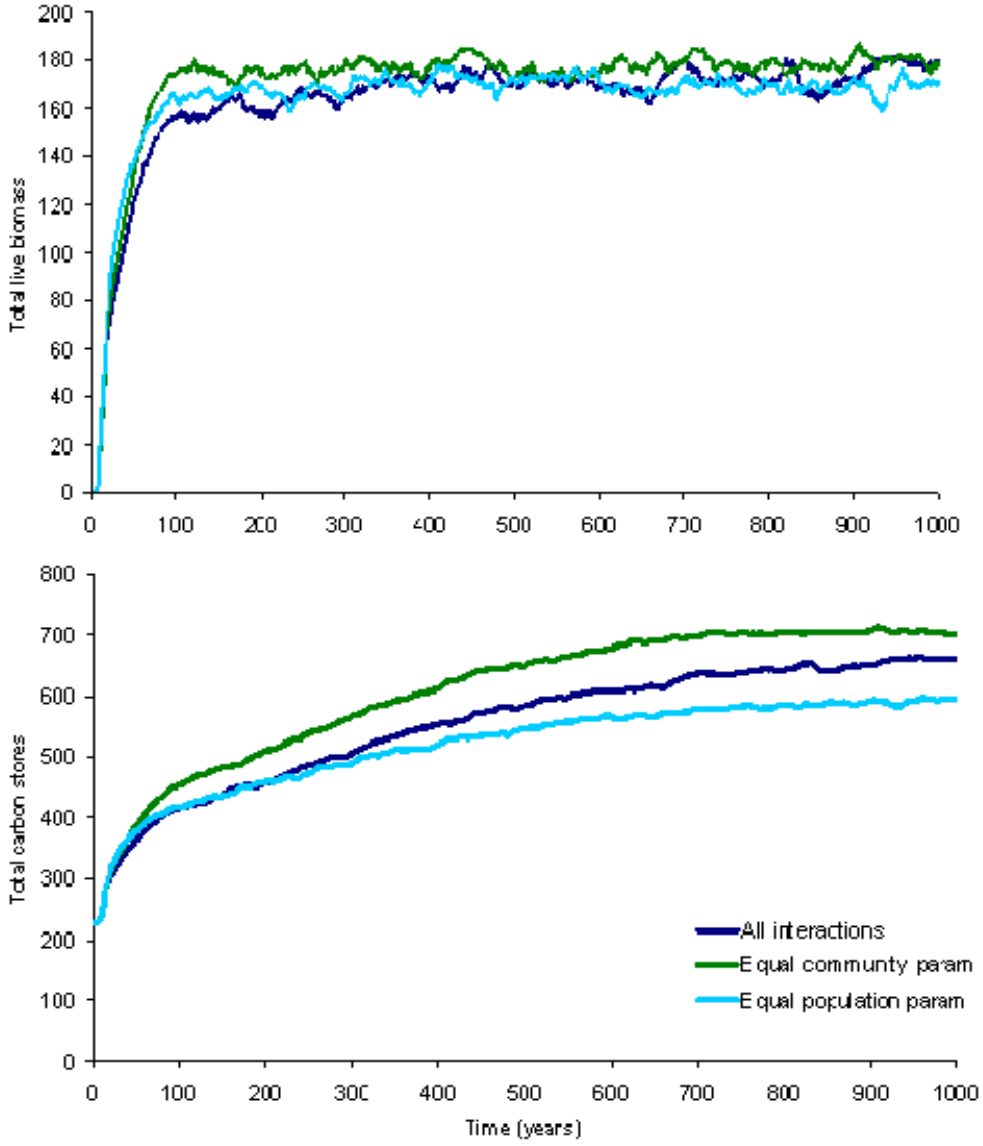

Figure 4.22. Total live biomass and total carbon stores from the previous set of simulations (Figure 4.20). In the "all interactions" simulation all parameters were different for all species. In the "Equal community param" simulation, community-related parameters were similar for all species. In the "Equal population param" simulation, population-related parameters were equal for all species.

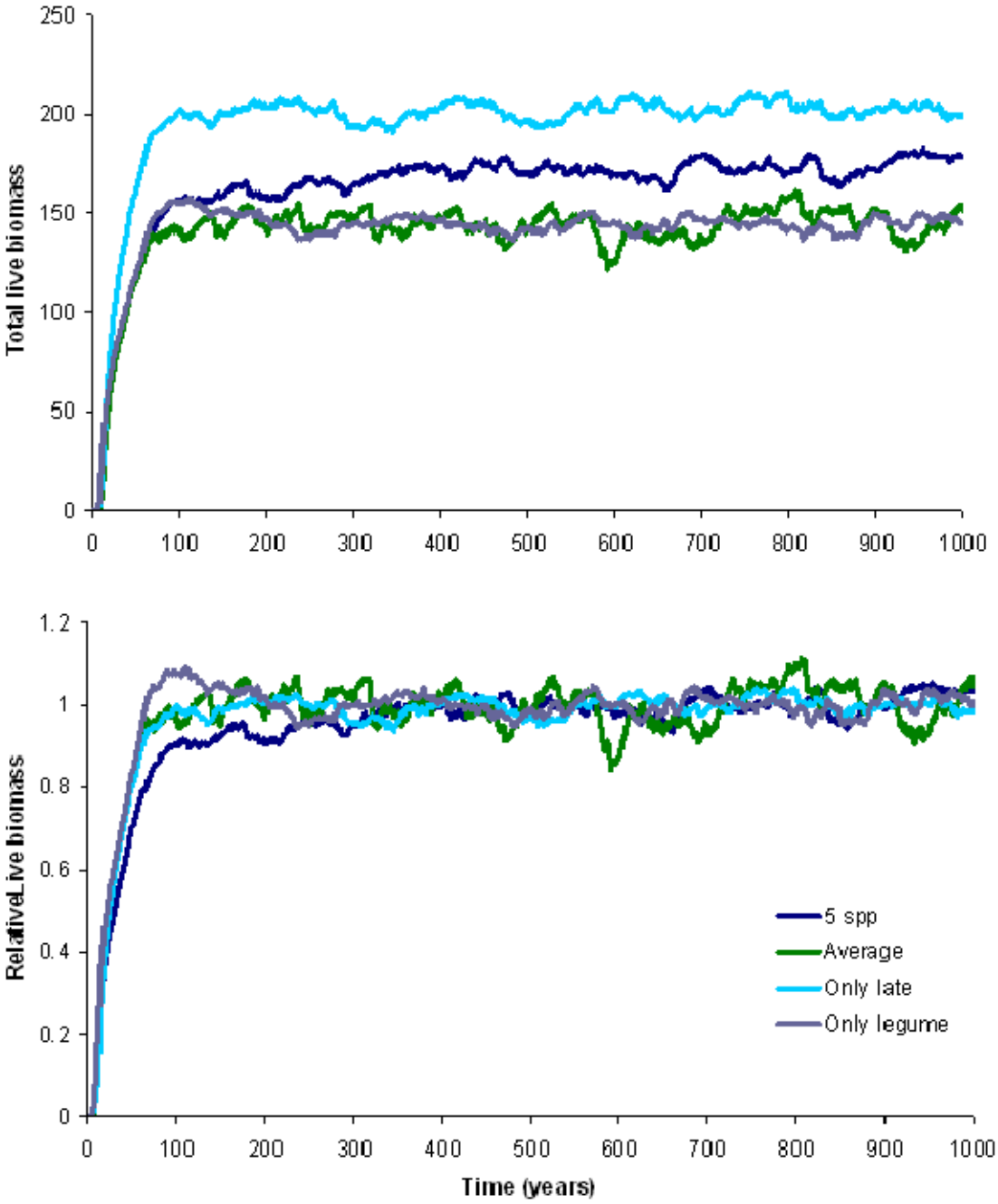

Figure 4.23. Total live biomass in absolute (upper) and relative units (lower) in simulations containing five different functional groups (5 spp), the average of the parameters from the five groups simulation (Average), only the late successional species (Only late), and only the legume species (Only legume).

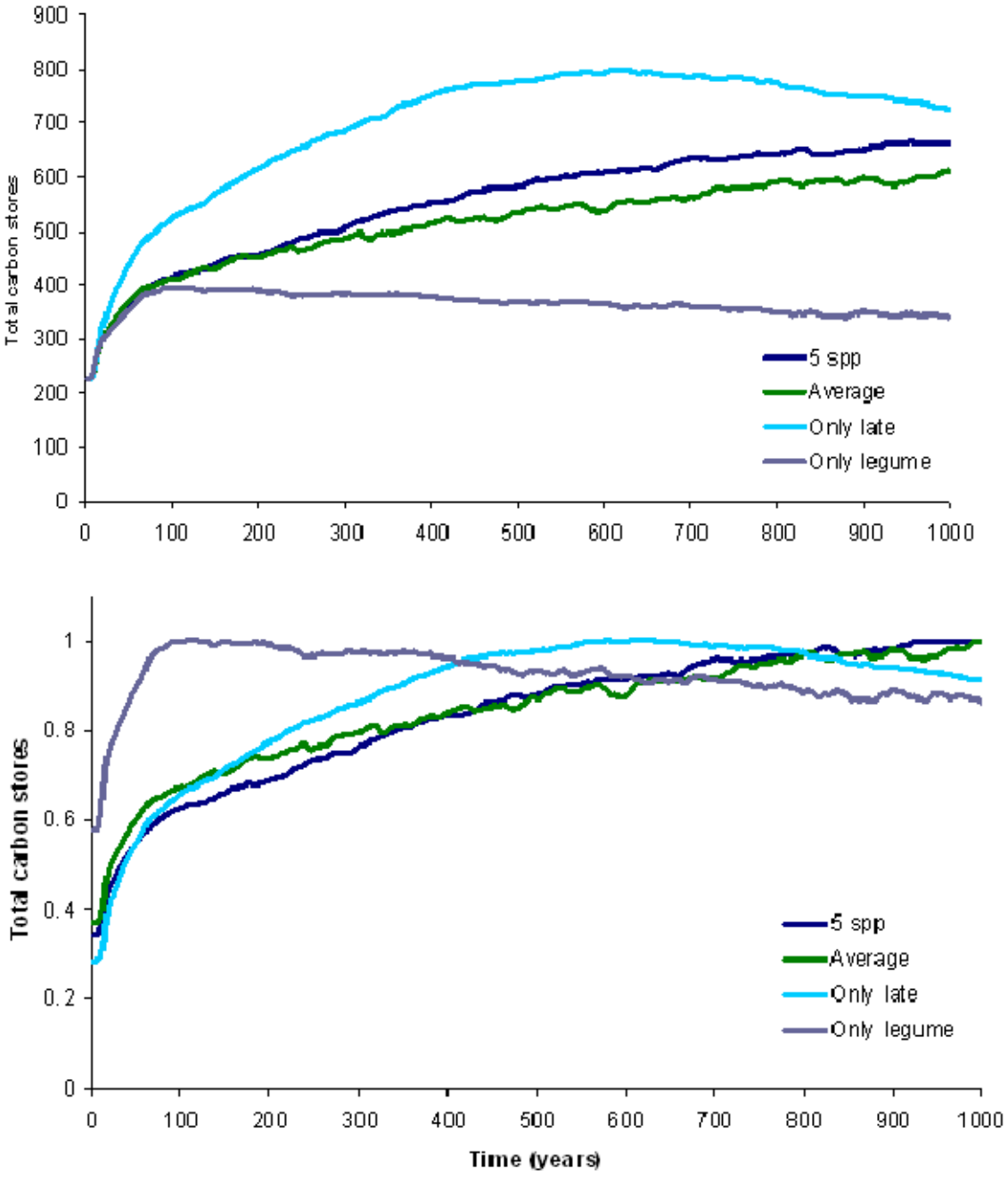

Figure 4.24. Total carbon stores in absolute (upper) and relative units (lower) in simulations containing five different functional groups (5 spp), the average of the parameters from the five groups simulation (Average), only the late successional species (Only late), and only the legume species (Only legume).

CHAPTER 5

CONCLUSIONS AND FUTURE DIRECTIONS

Carlos A. Sierra

Conclusions

In this research I studied aspects of the spatial and temporal variability of carbon dynamics in tropical forests of the Porce region in Colombia. I estimated average total carbon stocks as well as the uncertainty for a landscape composed of primary and secondary forests. I also estimated net ecosystem production for the primary forests of this region in two consecutive time intervals and evaluated these observations against hypothetical predictions. Finally, I used the STANDCARB model to assess effects of population and community processes on carbon dynamics at the ecosystem level. From these analyses I conclude that:

- Total carbon stocks in primary forests of the Porce region averaged 383.7 ± 43.0 Mg C ha^{-1}. Of this amount, soil organic carbon to 4 m depth represented 59%, total aboveground biomass 29%, total belowground biomass 10%, and necromass 2%.
- Total carbon stocks in secondary forests of the Porce region averaged 228.2 ± 11.5 Mg C ha^{-1}. Soil organic carbon to 4 m depth accounted for 84% of this amount, total aboveground biomass represented 9%, total belowground biomass 5%, and total necromass 1%.
- Spatial variation and measurement errors were important sources of uncertainty for quantifying the average carbon stock in this forest ecosystem. The number of sampling units can help to reduce the uncertainty associated with measurement errors, however spatial variation remains as an important component of

uncertanity. Spatial variability is an inherent property of the ecosystem which is often ignored in studies of carbon budgets. The uncertainty ranges reported in this study acknowledge the fact that carbon stores varies spatially.

- For the period 2000-2001, Net Primary Production (NPP) in primary forests of the Porce region was estimated as 12.6 ± 0.9 Mg C ha^{-1} yr^{-1}. Heterotrophic respiration (Rh) was estimated as -12.3 ± 2.0 Mg C ha^{-1} y^{r-1}, which resulted in a Net Ecosystem Production (NEP) of 0.34 ± 1.15 Mg C ha^{-1} yr^{-1}.
- For the period 2001-2002, NPP in primary forests was estimated as 12.93 ± 0.96 Mg C ha^{-1} yr^{-1} and Rh as -15.07 ± 1.70 Mg C ha^{-1} yr^{-1}. NEP was estimated as -2.15 ± 0.76 Mg C ha^{-1} yr^{-1} for this interval.
- Uncertainty results of NEP for the two periods studied did not provide sufficient evidence to reject the hypothesis that primary forests of this region are in carbon balance.
- Simulation with STANDCARB showed that processes at the level of populations, such as colonization and mortality can affect total carbon storage at the ecosystem level, can affect the variability of carbon accumulation, and can produce lags during the process of succession.
- Simulations with STANDCARB showed that processes at the level of communities can affect ecosystem carbon stores when species with different traits that are relevant in carbon dynamics are replaced.

Future directions

Large areas of tropical forests still remain relatively undisturbed storing important amounts of carbon. Deforestation processes threaten to release this carbon and at the same time reduce the biodiversity of the region. Knowledge about carbon stores in tropical forests can help to predict the consequences of deforestation and potential emissions of CO_2 to the atmosphere. Changes in carbon stores in tropical forests can now be valuated economically due to advances in international negotiations of the United Nations Framework on Climate Change. The economic value of carbon stores in tropical forests can, eventually, lead to their conservation and influence the policymaking process. For this reason it is very important to quantify total carbon stores in different regions throughout the tropics. Although there are many inventories of total aboveground biomass, carbon stores in other pools need to be quantified. For example, it is still not clear how total carbon stores vary across precipitation and temperature gradients, or how topography and fertility influence this ecosystem property.

The Porce region has become a major site of forest research in Colombia. Detailed information of carbon stores and fluxes is available for this region and it is, to my knowledge, on of the few sites in the tropics where a detailed carbon budget has been developed. Despite this, we do not know how carbon fluxes or stores vary over the long term. To this end it is imperative to keep monitoring total carbon stores over time and develop an infrastructure for long term studies. This also applies to carbon fluxes such as plant growth, litterfall, litter decomposition, root production, and soil respiration.

In addition to monitoring carbon stock and fluxes it is important to quantify environmental variables that can influence carbon dynamics. Some examples of types of questions that can be examined include: How lateral transfers such as DOC leaching and erosion correlate with topography? How different are the rates of biomass production and organic matter decomposition in fertile sites compared with less fertile sites? Is there any correlation between community diversity indexes and carbon stores? These are some examples of the type of questions that can be addressed by monitoring other variables that can be associated with carbon stocks and can provide useful information in identifying mechanisms.

Similarly, it is also important to develop manipulative experiments which can provide useful information on the major drivers of different ecosystem processes. Rain-exclusion experiments, for example, could provide very valuable information on possible effects of drought on forest productivity. Manipulation of diversity in experiments to see which ecosystem processes are influenced would also be a promising area of research.

Development of research at different levels of organization is also an important area for future research. From this study I found that population and community processes can have important effects on carbon dynamics. A further step in this area would be the acquisition of field data to compare with the predictions obtained in this modeling exercise. Particularly, I would be very interested in conducting research integrating the ecosystem process of decomposition with community composition. For example, would changes in community composition affect the decomposition process at the ecosystem

level, consequently modifying the net carbon balance of the ecosystem? This question could also be expanded to incorporate nutrient dynamics which would influence growth of plants.

In summary, future research on this topic for the Porce region should focus on: 1) establishing a program for the long-term monitoring of carbon stocks and fluxes; 2) expanding measurements to other variables of interest that can provide information on possible mechanisms to explain variations in carbon dynamics; 3) developing ground-based manipulative experiments to explore specific drivers of ecosystem function; and 4) integrate data and ideas through simulation models to explore new concepts.

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