

AN ABSTRACT OF THE DISSERTATION OF

Miguel Cifuentes-Jara for the degree of Doctor of Philosophy in Environmental Sciences presented on March 28 2008.

Title: Aboveground Biomass and Ecosystem Carbon Pools in Tropical Secondary Forests Growing in Six Life Zones of Costa Rica.

Abstract approved:

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Carbon sequestration in tropical secondary forests growing in all climates must be quantified to understand their potential role in adaptation and mitigation strategies of global climate change. Total aboveground biomass (TAGB), soil carbon, and total ecosystem carbon (TEC) were measured in 54 secondary forests growing along a broad bioclimatic gradient of 6 life zones, from lowland Dry to Premontane Rain forests in Costa Rica. The potential of regenerating secondary forests to offset carbon losses due to climate change-mediated primary forest degradation into the year 2100 was also determined.

TAGB ranged from $12 \text{ Mg}\cdot\text{ha}^{-1}$ ($5 \text{ MgC}\cdot\text{ha}^{-1}$) in a 9-yr Dry forest to $298 \text{ Mg}\cdot\text{ha}^{-1}$ ($143 \text{ MgC}\cdot\text{ha}^{-1}$) in a 60-yr Wet forest. TAGB and carbon were correlated with forest age and the ratio of potential evapotranspiration to precipitation. Secondary forests were predicted to reach $\text{TAGB} \geq 90\%$ of that in primary forest in 35 to 126 yrs. Mean soil carbon to 1 m ranged from 127 to $278 \text{ Mg}\cdot\text{ha}^{-1}$ in the Dry and Premontane Rain life zones. There was no correlation of soil C pools with age.

TEC was as high as $440 \text{ Mg}\cdot\text{ha}^{-1}$ in a 40-yr Premontane Rain forest. Maximum rates of TEC sequestration were highest ($14 - 33 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) in life zones with intermediate levels of precipitation and lowest (7 and $12 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) in the Dry and Premontane Rain life zones. Secondary forests were predicted to attain ecosystem C levels similar to that of primary forests in 44 – 105 yrs.

Based upon simulations of forest growth and the changing land area covered by differing life zones due to climate change, carbon losses from primary forests ranged from < 6 to 65 Tg under two different climate change scenarios for the year 2100. Secondary forests would need to cover 19% of each life zone to offset the larger flux of carbon into the atmosphere. Our modeling did not include additional carbon losses associated with changing disturbance regimes and other climate change responses. Results from this study underscore the value of secondary forests for their potential to sequester carbon across a diversity of tropical climates as a means of climate change mitigation.

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Aboveground Biomass and Ecosystem Carbon Pools in Tropical Secondary Forests

Growing in Six Life Zones of Costa Rica

by

Miguel Cifuentes-Jara

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

Miguel Cifuentes-Jara, Author

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Dr. J. Boone Kauffman was involved in the design, analysis, and writing of all chapters of this dissertation. Dr. R. Flint Hughes contributed ideas to the analysis. Ms. Judith Jobse was involved in the analysis. Dr. Vicente Watson was involved in the design, all stages of field work, and provided essential data for Chapter 4.

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ABOVEGROUND BIOMASS AND ECOSYSTEM CARBON POOLS IN
TROPICAL SECONDARY FORESTS GROWING IN SIX LIFE ZONES OF
COSTA RICA

INTRODUCTION

Secondary forests represent 35% of all existing tropical forests in the world (Emrich *et al.* 2000). In addition, Wright (2005) estimated secondary forests have replaced at least one of each six hectares of primary forest deforested in the 1990s and Wright & Mueller-Landau (2006) predicted that in the future most tropical forests will be secondary forests regenerating after previous clearing. In tropical America, secondary forests now cover at least 335 million ha, and it is suggested they exceed the area covered by primary forests in some countries (FAO 2005, Houghton *et al.* 2000). In Costa Rica, for example, 180 000 hectares are estimated to be under primary forest cover, while secondary forests cover 425 000 ha (Berti 2001). Likewise, in Puerto Rico, the area of “new forests” is also much greater than the area in primary forests (Lugo & Helmer 2004).

Because of their fast growth rates (Ewel 1971, Guariguata & Ostertag 2001) and increasing extent (Wright & Mueller-Landau 2006), secondary forests may function to improve degraded soils, maintain biodiversity, enhance water quality, and supply timber and non-woody products (Aide *et al.* 2000, Chazdon & Coe, 1999, Finegan 1992). In addition, secondary forests have a great potential to sequester C from the atmosphere (Brown & Lugo 1990, Silver *et al.* 2000). For example, Niles *et al.* (2002) estimated regenerating forests globally have the potential to accumulate 316 million Mg of C over a 10 year period, with 56% of that potential in Latin American countries.

Secondary forest research on tropical C dynamics has traditionally focused on moist and wet lowland climates (Brown and Lugo 1990, Finegan 1996, Guariguata & Ostertag 2001). A few recent studies have devoted attention to secondary forest dynamics in Tropical Dry (Kalacska *et al.* 2004, Romero-Duque *et al.* 2007, Vargas *et al.* 2008) and Montane climates (Fehse *et al.* 2002, Howorth & Pendry 2006, Nadkarni *et al.* 2004). Two major generalizations have emerged from this research: (1) Secondary forests have the potential to accumulate biomass and C pools similar to those in primary forests (Brown & Lugo 1990, Silver *et al.* 2000, Hughes *et al.* 1999); and (2) The severity and duration of previous land use affects the rate and pattern of secondary forest recovery (Fearnside & Guimarães 1996, Hughes *et al.* 1999, Uhl *et al.* 1988). However, the extent to which these generalizations are valid across a wide range of tropical climates is unclear (Guariguata & Ostertag 2001). Persistent questions related to biomass accumulation and carbon sequestration by tropical secondary forests addressed by this dissertation include:

1. How do rates and patterns of aboveground biomass recovery of tropical secondary forests differ across a diversity of climatic conditions encountered in the tropics?

There is considerable variation in the accumulation and partitioning of total aboveground biomass (TAGB) of wet and humid tropical secondary forests due to soil properties and land use history (Aide *et al.* 1995, Campo & Vásquez-Yanes 2004, Fearnside & Guimarães 1996, Hughes *et al.* 1999, Saldarriaga *et al.* 1988, Uhl *et al.*

1988). However, comparative datasets from forest types growing in many prevalent tropical climates are lacking and the differences in methods and data analysis often make comparisons uncertain. These are serious limitations because reliable site-specific studies are necessary for large scale estimation of biomass and C sequestration.

2. How long do tropical secondary forests growing along a diversity of climatic conditions require to accumulate aboveground biomass and sequester C pools similar to those found in primary forests?

It is important to establish how long it takes for secondary forests accumulate biomass and sequester C pools equivalent to that in primary forests to properly assess restoration goals. Current estimates of the time required by secondary forests to accumulate biomass similar to that measured in primary forests range from 45 to ~ 200 years depending on the inherent site fertility and the intensity of previous land use history (Molina Colón & Lugo 2000, Saldarriaga *et al.* 1988, Uhl *et al.* 1988). However, given the diversity of biotic conditions found in the tropics, research is also needed to further clarify the degree to which these rates may be modified through future climatic variation.

3. What is the role of secondary forest soils in the sequestration of atmospheric C?

Tropical soils contain as much as 474 Pg of C, or 20% of total global soil C storage (Jobbágy & Jackson 2000). Increased soil C pools as secondary forests age have been documented in a few studies (Brown & Lugo 1990, Silver *et al.* 2000). However, data from Hughes *et al.* (1999), de Koning (2003), and Schedlbauer and Kavanagh (2008) showed few changes in soil C pools through secondary succession following agricultural abandonment. In a recent review, Guo & Gifford (2002) documented changes in soil C ranging from ~ -40 to 5% after conversion of pasture to secondary forest. Clearly, more research is needed to further clarify the role of secondary forest soils in the sequestration of C, especially when considered as part of the land-use continuum commonly found in tropical landscapes.

4. At the ecosystem level, what is the potential of tropical secondary forests to sequester C?

Aboveground and soil C pools in tropical secondary forests have been previously quantified (Fearnside & Guimarães 1996, Feldpausch *et al.* 2004, Saldarriaga *et al.* 1988). However, simultaneous assessments of total ecosystem C storage and change of that storage over time are extremely limited (Clark 2004, Hughes *et al.* 1999, Sierra *et al.* 2007, Vargas *et al.* 2008). Moreover, an explicit assessment of the ecosystem-level potential (above ground and soil C pools) of secondary forests to sequester C over time across a broad tropical climatic gradient (*i.e.* Tropical Dry to Tropical Wet and Montane forests) has yet to be undertaken.

5. Given ongoing climate change, can secondary forests sequester enough C to offset losses from primary forests?

Ongoing warming and drying climate can potentially alter forest dynamics and result in large losses of C from primary forests into the atmosphere (Clark 2004). Secondary forests have been shown to sequester large amounts of carbon (Silver *et al.* 2002) and could offset these losses. However, because of changing climate, secondary forests may no longer have the capacity to accumulate C to historical levels (Chazdon *et al.* 2007, Feldpausch *et al.* 2007, Harris *et al.* 2006). It is thus necessary to determine the extent to which secondary forests growing in a variety of tropical climates will maintain their potential to act as carbon sinks and offset carbon losses from primary forest degradation due to climate change.

This study was designed to address these questions by (1) quantifying the amount and structure of TAGB, TAGC, and total ecosystem C (total above- and below ground C pools to 1 m depth) in secondary forest chronosequences in six life zones of Costa Rica, (2) describing the patterns of biomass accumulation and C sequestration of secondary forests and calculating the time required for them to reach levels of biomass and C similar to those found in primary forests, and (3) determining the potential C balance in forested tropical landscapes of Costa Rica by predicting the amount of C that would be emitted by primary forests and sequestered by secondary forests under

ongoing climate change into the year 2100. If these objectives are satisfied, this will be the first study to provide baseline data on changes in aboveground biomass accumulation (Chapter 2), and ecosystem-level C sequestration (Chapter 3) for secondary forests growing in a diversity of tropical climates. In addition, this study will test the notion that secondary forests have the potential to offset landscape-scale C losses from primary forests even under changing climatic conditions (Chapter 4).

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CHAPTER 2

TOTAL ABOVEGROUND BIOMASS ACCUMULATION OF SECONDARY FORESTS GROWING ALONG A BIOCLIMATIC GRADIENT IN COSTA RICA

Abstract

Knowledge of biomass accumulation rates is necessary to understand the potential role of tropical forest ecosystems in mitigating global change. Tropical secondary forests are rapidly becoming an abundant land cover in many tropical regions as agricultural lands are abandoned. As a result, secondary forests may play an important role in attempts to mitigate climate change through the fixation of C in tropical forest carbon management. We measured total aboveground biomass (TAGB) of 54 secondary forests growing along a bioclimatic gradient encompassing six life zones of Costa Rica from Tropical Dry to Premontane Rain forests. Maximum rates of TAGB accumulation ranged from $5.7 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in the Dry life zone to $11.4 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in the Wet life zone. In less than 60 yr, Premontane Rain and Wet life zone forests accumulated TAGB between 250 to $300 \text{ Mg}\cdot\text{ha}^{-1}$. Secondary forests in the Moist and Premontane Wet Transition to Basal life zones accumulated up to $200 \text{ Mg}\cdot\text{ha}^{-1}$ in 27 yr, while secondary forests in the Dry life zone accumulated only $160 \text{ Mg}\cdot\text{ha}^{-1}$ in 82 yr. Based on a non-linear growth function we predicted secondary forests attain $\geq 90\%$ of TAGB in primary forests within 35 years in the Dry life zone and 124 years in the Wet life zone. TAGB was accurately predicted by basal area of stems $\geq 10 \text{ cm dbh}$, suggesting a simplified relationship may be used to estimate TAGB from existing data *in lieu* of intensive field inventories. In the context of ameliorating global climate change, regenerating secondary forests in the productive wet life zones would yield greater benefits per unit area because of larger potential biomass pools and greater

initial rates of sequestration. However, climate change is likely to result in different future rates of sequestration than in this study and thereby require reevaluation of growth potential.

Introduction

Secondary forests are increasingly important components of tropical landscapes. Emrich *et al.* (2000) estimated secondary forests represent 35% of all tropical forests in the world and this number has no doubt increased over the last decade. In tropical America, secondary forests now cover at least 335 million hectares, exceeding the area covered by primary forests in some countries (FAO 2005, Houghton *et al.* 2000). In Costa Rica, for example, 180 000 hectares are estimated to be under primary forest cover, while secondary forests cover 425 000 ha (Berti 2001). Likewise, in Puerto Rico, the area of “new forests” is also much greater than the area in primary forests (Lugo & Helmer 2004). Because of their fast growth rates (Ewel 1971, Guariguata & Ostertag 2001, Silver *et al.* 2000) and increasing area, secondary forests provide many valuable ecosystem services. They improve degraded soils, conserve biodiversity, improve water quality, and provide wood and non-timber forest products. In addition, they have the potential to accumulate biomass and sequester C from the atmosphere (Aide *et al.* 2000, Chazdon & Coe, 1999, Finegan 1992, Lugo *et al.* 2004, Maass *et al.* 2005, Saldarriaga *et al.* 1988, Silver *et al.* 2000, Wright & Mueller-Landau 2006).

Traditionally, research on secondary forests has focused on quantifying recovery of floristic and structural characteristics (Aide *et al.* 1995, Denslow 2000, Finegan 1996, Lieberman *et al.* 1996, Purata 1986), biomass (Alves *et al.* 1997, Hughes *et al.* 2000, Saldarriaga *et al.* 1988, Uhl *et al.* 1988), and C pools (Fearnside & Guimarães 1996, Hughes *et al.* 1999, Johnson *et al.* 2001) in Tropical Moist and Tropical Wet secondary forests. Recently, research has expanded to include Tropical Dry (Jaramillo *et al.* 2003, Kalacska *et al.* 2005, Romero-Duque *et al.* 2007, Vargas *et al.* 2008) and Montane forests (Fehse *et al.* 2002, Howorth & Pendry 2006, Nadkarni *et al.* 2004). Despite efforts expended to document variation in growth patterns of tropical secondary forests (Aide *et al.* 1995, Campo & Vásquez-Yanes 2004, Fearnside & Guimarães 1996, Hughes *et al.* 1999, Saldarriaga *et al.* 1988, Uhl *et al.* 1988), data are lacking to contrast secondary forests growing under different climates.

A comprehensive assessment of the rates of biomass accumulation across broad tropical climatic gradients (*i.e.*, from lowland Tropical Dry to Montane Rain forests) is clearly needed. Here we report research that provides a baseline to quantify the accumulation of TAGB biomass pools by secondary forests growing across such a gradient. Our objectives were: (1) to quantify the size and patterns of accumulation of total aboveground biomass pools in secondary forests growing in six life zones in Costa Rica, (2) to determine the time required for secondary forests to match biomass pools in primary forests, and (3) to develop equations using a commonly available

forest inventory variable, basal area, to predict total aboveground biomass and simplify the estimation of TAGB. Our underlying assumption was that, given enough time, secondary forests will achieve a total aboveground biomass comparable to that measured in primary forests. In addition, we expected the rates, as well as the maximum amount of biomass accumulated would be higher in environments with increased precipitation.

Methods

Study Area

This study was conducted in secondary forests of six life zones located throughout Costa Rica, Central America. Costa Rica is an ideal study area because, within its relatively small territory (51 000 km², Bolaños and Watson 1993), it contains broad gradients of temperature and rainfall, as well as land-uses and soil types that encompass much of the conditions found elsewhere in the Neotropics. Costa Rica was once almost 100% forested (Keogh 1984). However, between the 1960s and late 1970s, high production of cattle for beef exports promoted extensive deforestation in the country (Arroyo-Mora *et al.* 2005). Most of the primary forest clearing occurred in the Tropical Dry and Moist life zones of Costa Rica, with deforestation rates reaching up to 10%·yr⁻¹ prior to 1977 (Sader & Joyce 1988). By 1989, 48% of Costa Rica had

been converted from forest to pasture (Arroyo-Mora *et al.* 2005). However, declining beef prices and increasing public awareness of the ecological impacts of deforestation led to the abandonment of pastures and the establishment of a national system of protected areas, which now covers 25% of the country (Kleinn *et al.* 2002). It is estimated that 48% of Costa Rica is now under forest cover, much of which may be secondary forests (Kleinn *et al.* 2005, Vicente Watson, unpublished data). Secondary forest growth throughout the country offers many opportunities for promoting biomass accumulation and C sequestration.

Site Selection

The Holdridge Life Zone System (Holdridge 1967) was used as the basis for partitioning forest types along environmental gradients. The six life zones in which secondary forests were sampled included Tropical Dry forest, Tropical Moist forest, Premontane Wet Transition to Basal forest (Atlantic and Pacific rainfall regimes), Tropical Wet forest, and Premontane Rain forest (Figure 2.1). For the purpose of this research, we refer to these life zones as Dry, Moist, Premontane Wet - Pacific, Premontane Wet - Atlantic, Wet, and Premontane Rain, respectively. Also, we refer to the first three life zones as “Drier” because of the occurrence of a distinct dry season (when mean monthly rainfall is < 100 mm) and the dominance or co-dominance of deciduous tree species in the canopy. We term the remaining life zones as “Wetter” because precipitation occurs throughout the year and evergreen tree species dominate

the forest. Collectively, these life zones cover approximately 55% of the country (Table 2.1) and form a bioclimatic gradient from warm and dry to cool and wet forests.

Chronosequences spanning the age range of secondary forests within a life zone were sampled. We separated the Premontane Wet Transition to Basal life zone into Atlantic and Pacific regions and sampled one chronosequence in each (Table 2.2). Although both regions have the same life zone classification (Holdridge 1967), the Pacific region of Costa Rica has a distinct dry season (*i.e.* average monthly precipitation < 100 mm for ≥ 3 months), which places limitations on plant growth and results in contrasting forest physiognomies when compared to Premontane Wet - Atlantic forests (Holdridge *et al.* 1971).

Secondary forests in each life zone were selected by overlaying the 1:200 000 Life Zone System Map for Costa Rica (Bolaños and Watson 1993) with the 1992 Land Use Map (MAG 1992) in a GIS. We sampled 54 secondary forests in the six selected life zones (Table 2.2). Once sites were located, we interviewed local residents to obtain information on the range of secondary forest ages in a life zone. The range of secondary forest ages was not equal among life zones because of differences in patterns of land use and abandonment across Costa Rica. For example, secondary forest age ranged from 6 to 82 yr in the tropical Dry forest, and between 8 months to 35 years in the tropical Wet forest life zones (Table 2.2).

The pool of potential secondary forest sites available for sampling was further narrowed by having to meet three criteria. First, only sites previously used as pastures, were chosen. Second, logged secondary forests were not considered. Finally, patches of secondary forests had to be ≥ 1.5 times larger than our plot size (0.25 ha).

Table 2.1. Life Zones selected for this study, areal cover in Costa Rica (ha), percent of the total area of Costa Rica that they cover, range of secondary forest ages (years), and number of plots sampled. Total area of Costa Rica is $\sim 51015 \text{ km}^2$. Data from Bolaños & Watson (1993).

Life Zone	Area (km^2)	Percent of Costa Rica	Age range (years)	Sample size
Dry forest	1056.08	2.07	0 – 82	10
Tropical Moist forest	6954.91	13.63	0 – 40	10
Tropical Premontane Wet forest, Transition to Basal	7440.59	14.59	0 – 22	13
Tropical Wet forest	8462.84	16.59	0 – 60	11
Premontane Rain forest	4380.06	8.59	0 – 50	10
Total	31755.79	55.47		54

We recognize sampling 5 – 10 secondary forest sites per life zone is a small number to predict rates of biomass accumulation. We also recognize that there are inherent limitations to the chronosequence approach in regard to substituting spatial differences in stand age for measurements taken over time in a given location (Dewalt *et al.* 2000, Schedlbauer & Kavanagh 2008. Data from this study, nevertheless, should provide reasonable initial estimates of the patterns of biomass accumulation in different life zones.

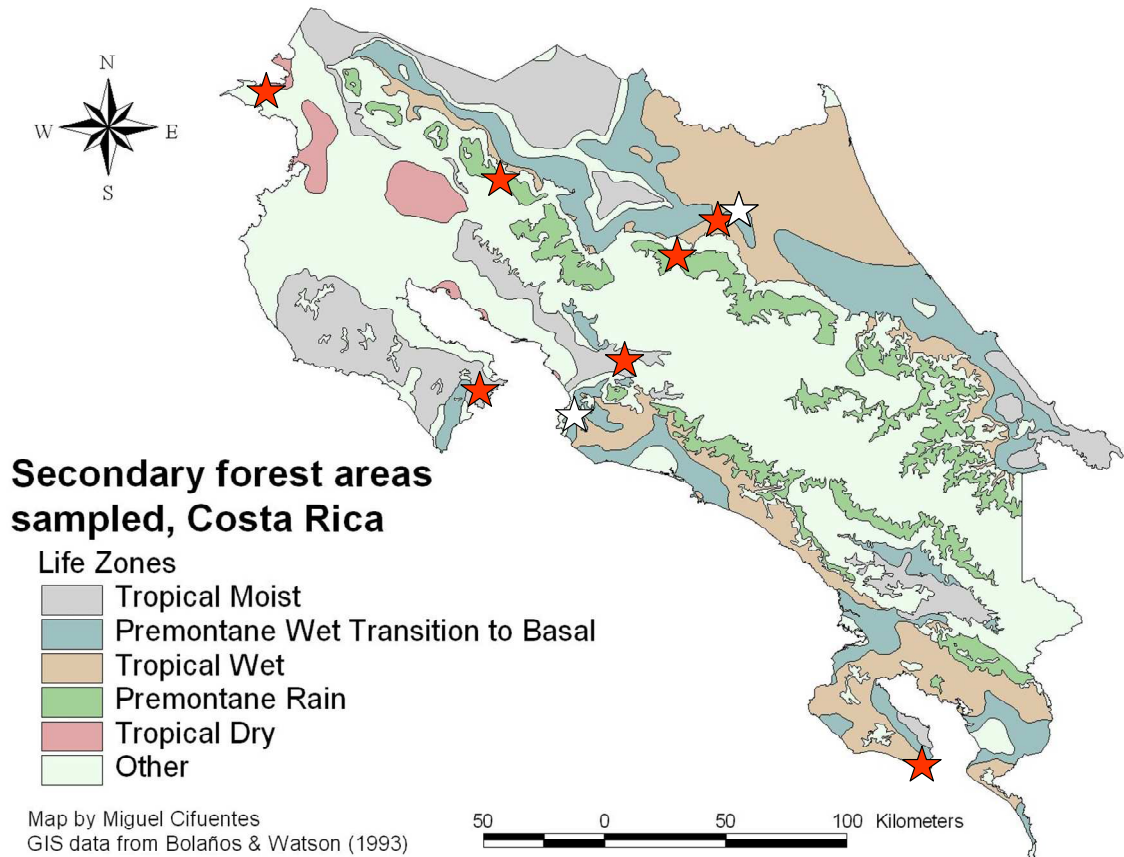


Figure 2.1. Location of secondary forest study areas in six life zones of Costa Rica. Stars represent general sampling areas where secondary forests of different ages were sampled. Open stars represent the separation of the Premontane Wet Transition to Basal life zone into Pacific and Atlantic regions because of physiognomic differences between the forests.

Total Aboveground Biomass

To quantify TAGB, we used a component analysis similar to that described by Hughes *et al.* (1999). We sampled all aboveground forest components in a 2500 m² (50 x 50 m) nested plot (Figure 2.1). This plot size provided an adequate sampling area to

characterize TAGB and successional trajectories (Chave *et al.* 2004, Hughes *et al.* 1999, Saldarriaga 1998) and was compatible with the small size of secondary forest patches present in Costa Rican landscapes. In all plots, the diameters at breast height (dbh, measured at 1.30 m height or 10 cm above any stem irregularities) of all trees, palms, and lianas ≥ 10 cm dbh rooted within the 50 x 50 m plots were measured. In addition, the mass of dead trees and palms was calculated from measurements of both dbh and height of each snag; the latter obtained with a clinometer. The diameter and height of all stumps were also measured inside the main plot. The species, growth form (*e.g.* tree, liana/vine, palm, snag), and whether the stem was dead or alive, were also recorded. Samples from plants not identified to species in the field were taken to the Tropical Science Center (TSC) or the Instituto Nacional de Biodiversidad (InBio) for identification by taxonomists. We used species names and live/dead status to assign the appropriate wood specific gravity data for biomass calculations (Table 2.3).

Table 2.2. Location and physical characteristics of secondary forest study sites in six life zones of Costa Rica.

Life Zone	Plot name	Age (yrs)	Latitude (dec)	Longitude (dec)	Slope (%)	Elevation (m)	Temperature (°C)	Precipitation (mm)	Soil type
Tropical Dry	Pitahaya	9	10.8732	-85.5788	2	243	26.2	1613	Entisol
	Bebedero	10	10.8883	-85.6000	4	280	25.9	1613	Entisol
	Pocosol	10	10.8889	-85.6004	3	278	25.9	1613	Entisol
	Mal Uso	14	10.8470	-85.6143	5	307	25.8	1530	Entisol
	Casita	16	10.8757	-85.5853	10	300	25.8	1596	Entisol
	Deep Throat	16	10.8266	-85.6134	15	288	25.9	1513	Entisol
	Firebreaks	17	10.8705	-85.5946	2	148	26.8	1573	Entisol
	Príncipe	22	10.8533	-85.6081	2	273	26.0	1563	Entisol
	Naranjo	26	10.7992	-85.6485	1	23	27.6	1630	Entisol
	Buen Uso	27	10.8393	-85.6152	16	321	25.7	1556	Entisol
	El Pozo	82	10.8375	-85.6147	15	340	25.6	1556	Entisol
Tropical Moist	Downey	0.42	9.8586	-84.5241	35	120	27.2	2700	Alfisol
	Valle Azul	7	9.7793	-84.9552	60	37	27.7	2208	Alfisol
	Caballos	7	9.8446	-84.5281	10	132	27.1	2900	Alfisol
	Divino	9	9.7876	-84.9392	63	43	27.7	2208	Alfisol
	Iguana	13	9.8451	-84.5292	20	160	26.9	2900	Alfisol
	Quesera	16	9.8019	-84.9051	12	30	27.7	2042	Alfisol
	Dubya	20	9.8397	-84.5478	14	168	26.9	2925	Alfisol
	El Tanque	28	9.7908	-84.9244	65	43	27.7	2092	Alfisol
	Santa Teresa	30	9.7855	-84.9498	50	51	27.6	2308	Alfisol
	Chonco	40	9.8401	-84.5403	20	53	27.6	2900	Alfisol
Tropical	Yucal	2	9.7725	-84.6183	20	244	26.4	3000	Ultisol
Premontane Wet,	Chupadero	6	9.7761	-84.6180	30	45	27.6	3000	Ultisol
Transition to	Lapas	10	9.7792	-84.6058	30	46	27.6	3500	Inceptisol
Basal, Pacific	Hotel	15	9.7601	-84.6145	17	38	27.7	2950	Ultisol
	Luciano	22	9.7713	-84.6140	30	101	27.3	3100	Ultisol
Tropical	Cano	3	10.4214	-84.1618	27	224	24.3	3900	Inceptisol
Premontane Wet,	SAT 900	6	10.4315	-84.0205	10	74	25.2	3892	Inceptisol
Transition to	Con Permiso	10	10.4556	-84.1763	15	141	24.8	3800	Inceptisol
Basal, Atlantic	SAT 1000	15	10.4319	-84.0218	2	76	25.1	3892	Inceptisol
	Pao	21	10.4310	-84.0157	8	65	25.2	3892	Inceptisol
	Cascada	26	10.3948	-83.9868	45	92	25.1	3900	Inceptisol
	Sábalo	27	10.4165	-84.0029	30	74	25.2	3892	Inceptisol
	SHO 750	32	10.4170	-84.0036	2	70	25.2	3892	Inceptisol
Tropical Wet	Terciopelo	0.7	10.4270	-84.0950	26	140	24.8	3942	Ultisol
	TUVA	1	8.4055	-83.3398	2	46	27.2	4250	Ultisol
	Culebra	3	10.4248	-84.0965	40	158	24.7	3942	Ultisol
	La Huerta	6.5	8.4086	-83.3363	12	68	27.1	4300	Ultisol
	Don Juan	9	10.4553	-84.0665	24	143	24.8	3967	Ultisol
	Tirimbina	18	10.4025	-84.1125	35	261	24.1	4017	Ultisol
	Piro	20	8.4055	-83.3408	4	15	27.4	4200	Ultisol
	Pumilio	25	10.5060	-84.0561	2	79	25.1	4017	Inceptisol
	4 Ríos	29	10.3888	-84.1327	30	248	24.2	3967	Inceptisol
	Caliente	35	8.4053	-83.3372	4	74	27.0	4300	Ultisol
	Palma Real	60	8.3961	-83.3374	20	10	27.4	4200	Inceptisol

Table 2.2. (Continued)

Life Zone	Plot name	Age (yrs)	Latitude (dec)	Longitude (dec)	Slope (%)	Elevation (m)	Temperature (°C)	Precipitation (mm)	Soil type
Premontane Rain	Volcán	0.5	10.2811	-84.1483	40	937	20.4	5042	Ultisol
	Vírgen María	10	10.2822	-84.1502	30	992	20.1	5002	Entisol
	Alemán	15	10.3019	-84.7408	30	962	21.6	5800	Andisol
	Cornelio	19	10.2970	-84.7515	20	1044	21.1	5500	Andisol
	Milpa	20	10.2865	-84.1761	25	937	20.4	5002	Entisol
	Dos Ases	20	10.2975	-84.7621	27	1150	20.4	5400	Andisol
	Cambronero	30	10.2989	-84.7665	25	1200	20.1	5300	Andisol
	Hondura	35	10.2844	-84.1757	15	863	20.8	5002	Entisol
	Vargas	40	10.2981	-84.7684	18	1220	20.0	5300	Andisol
	Kraven S.A.	50	10.2652	-84.1565	25	1047	19.8	4902	Ultisol

Notes: Age refers to the number of years since agricultural practices stopped in the sampled areas. Slope was taken along the aspect of the site. Temperature and precipitation are mean annual values interpolated from nearest meteorological station data (Castro 1992). Soil type was obtained from Vásquez Morera (2003). Latitude, longitude and elevation are from GPS readings taken on site.

We measured the diameter of all trees < 10 cm dbh and taller than 1.30 m inside 1 x 15 m subplots at each sampled site. These small tree subplots were located on the periphery of the main plot and randomly oriented (n= 8 per plot, Figure 2.2). Live stems < 1.30 m in height (saplings) were considered part of the surface layer and collected in 0.5 x 0.5 m microplots adjacent to each small tree subplot and located 2 m away from the subplot's origin (n= 8 per plot). We also collected dead saplings, seedlings, and all downed material (litter) found inside this microplot (Figure 2.2). Litter consisted of leaves, bark fragments, seeds, flowers, fruits, and small woody stems \leq 2.54 cm in diameter. Downed wood (*i.e.* dead wood material with diameter > 2.54 cm) was measured along two 15 m, randomly oriented, transects located at 8 points in the periphery of the plot (n= 16, Figure 3.1) using the planar intersect technique (Brown & Roussopoulos 1974, Van Wagner 1968). We did not quantify

biomass of epiphytes because they represent 0.11% of TAGB in secondary forests (Nadkarni *et al.* 2004)

Dry mass of each ecosystem component was calculated using a combination of life zone-specific allometric equations developed specifically for each biomass component (Table 2.3). Litter biomass was determined directly from oven-dried field samples. All plant samples were oven-dried to constant mass at 65 °C and then weighed. Species-specific wood density (Sg) values (Chichignoud *et al.* 1990; Chudnoff 1984; Fearnside 1997; Malavassi 1992; Mueller-Landau unpublished database; Wiemann and Williamson 1989; Wiemann and Williamson 1989a, Brown *et al.* 1989) were used to determine tree biomass (Table 2.3). Whenever species-specific Sg values were not available, we used the average Sg for its genus, or more rarely, its family. When that was not possible, we used an average value of $0.59 \text{ g}\cdot\text{cm}^{-3}$ (Hughes *et al.* 1999). Biomass of downed wood was calculated using the planar intersect technique, after correcting for slope (Van Wagner 1968; Brown and Roussopoulos 1974). Life zone-specific downed wood density values were determined by a companion study (Kauffman, J. B. unpublished data). Total aboveground biomass was obtained by adding biomass values of all aboveground ecosystem components.

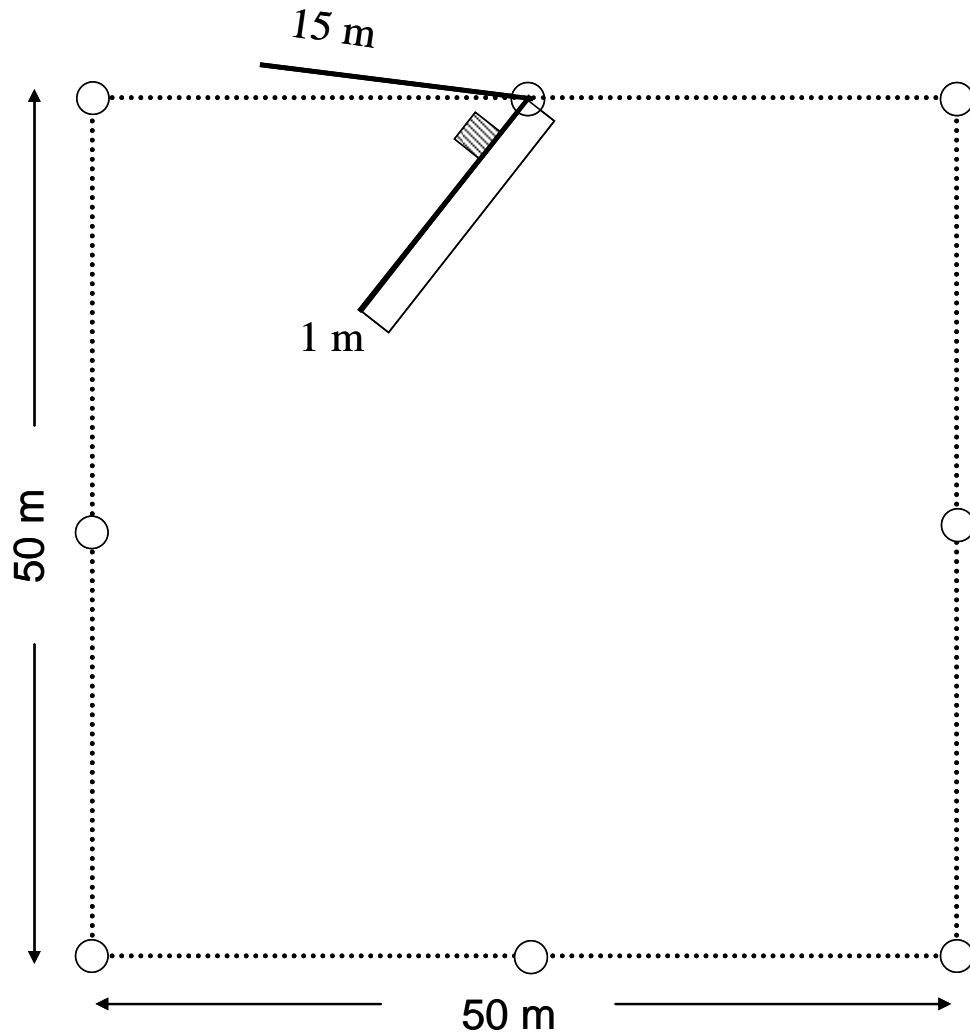


Figure 2.2. Plot layout to quantify total aboveground biomass (TAGB, $\text{Mg}\cdot\text{ha}^{-1}$) in secondary forests of six life zones in Costa Rica. Plot limits are shown in dotted lines. Although only a pair of random-direction downed wood transects (solid lines) and small tree subplots ($\text{dbh} < 10$ cm, open rectangle) are represented here, a similar pair originated at all locations marked with open circles ($n = 16$ downed wood transects and $n = 8$ small tree subplots). A forest floor microplot (filled square) was associated with each small tree subplot and located 2 from the origin of the small tree subplot ($n = 8$).

Table 2.3. Equations to determine aboveground biomass in tropical secondary forests. All biomass values are expressed as dry mass ($\text{Mg}\cdot\text{ha}^{-1}$).

Component	Equation	R ²	Life Zone	Source
Tree height	$8.5513*\ln(D)-13.384$	0.61	Tdf	Kauffman, J.B. unpublished data
Tree height	$9.8279*\ln(D)-11.775$	0.74	Tmf	Kauffman, J.B. unpublished data
Tree height	$13.185*\ln(D)-20.407$	0.76	Twf	Kauffman, J.B. unpublished data
Tree height	$10.601*\ln(D)-13.493$	0.76	Pwf	Kauffman, J.B. unpublished data
Tree height	$12.032*\ln(D)-16.612$	0.63	Rf	Kauffman, J.B. unpublished data
Trees > 10 cm dbh	$(0.112*((Sg*(D^2)*H)^{0.916}))*10^{-3}$	na	Tdf	Chave <i>et al.</i> (2005)
Trees > 10 cm dbh	$(0.0509*(Sg*(D^2)*H))*10^{-3}$	na	Tmf, Pwf-P	Chave <i>et al.</i> (2005)
Trees > 10 cm dbh	$(0.0776*((Sg*(D^2)*H)^{0.94}))*10^{-3}$	na	Twf, Pwf-A, Prf	Chave <i>et al.</i> (2005)
<i>Cecropia</i> > 10 cm dbh (wood)	$\exp(-3.78+0.95*\ln(D^2)+1.00*\ln(H))*10^{-1}$	0.88	All	Uhl <i>et al.</i> (1988)
<i>Cecropia</i> > 10 cm dbh (leaf)	$(-0.56+0.02(D^2)+0.04*H))*10^{-1}$	0.98	All	Uhl <i>et al.</i> (1988)
Standing dead stems > 10 cm dbh	$\pi((D/2)^2)*H*0.42$	none	All	Hughes <i>et al.</i> (1999)
Trees < 10 cm dbh	$(\exp(4.9375+1.0583*\ln(D^2)))*CF*10^{-6}$	0.93	All	Hughes <i>et al.</i> (1999)
Dead trees < 10 cm dbh	$(\exp(4.6014+1.1204*\ln(D^2)))*CF*10^{-6}$	0.95	All	Hughes <i>et al.</i> (1999)
Palms < 10 cm dbh	$((\exp(0.9285*\ln(D^2)+5.7236)*1.05)*10^{-6}$	0.39	All	Cummings <i>et al.</i> (2002)
Palms > 10 cm dbh	$(7.7*(H)+4.5)*10^{-3}$	0.90	All	Frangi & Lugo (1985)
Stemless palm fronds	$\exp(2.499762+(0.159766*D))*10^{-6}$	0.91	Tmf, Twf	This study
Lianas	$10^{(0.12+0.91*\log_{10}(BA))}*10^{-3}$	0.82	Pwf, Rf	Putz (1983)
Lianas	$\exp(0.07+2.17*\ln(D))*10^{-3}$	0.95	Tdf, Tmf	Gerwin & Farias (2000)
Downed wood > 2.45 cm diameter	$Sg((\pi^2*\sum(D^2)*Cs)/8L)*10^2$	--	All	Van Wagner (1968), Brown & Roussopoulos (1974)
<i>Heliconia</i> leaf	$10^{(-0.84237+(1.16617*(\log_{10}(H*R))))}*1.1028*10^{-6}$	--	All	Ewel, J.J. unpublished data
<i>Heliconia</i> stem	$10^{(-1.12141+(1.34261*(\log_{10}(H*R))))}*1.1496*10^{-6}$	--	All	Ewel, J.J. unpublished data
<i>Heliconia</i> fruit	$10^{(-0.03164+(0.66521*(\log_{10}(H*R))))}*1.37031*10^{-6}$	--	All	Ewel, J.J. unpublished data
Litter	Oven dry mass	--	All	Hughes <i>et al.</i> (1999)

Notes: BA= basal area (cm^2); Cs= slope correction factor, square root of $[1+(\% \text{ slope}/100)^2]$; D= diameter at breast height (cm); $\sum(D^2)$ = sum of (downed wood diameters)² (cm^2); H= height (m); L= transect length (cm); N= number of pieces of downed wood intersected per transect; R= number of resprouts; Sg= specific gravity of wood ($\text{g}\cdot\text{cm}^{-3}$); Tdf= Tropical Dry forest; Tmf= Tropical Moist forest; Twf= Tropical Wet forest; Pwf-P: Premontane Wet Transition to Basal forest; Pacific, Pwf-A: Premontane Wet Transition to Basal forest, Atlantic; Prf= Premontane Rain forest. *Heliconia* biomass calculated as the sum of *Heliconia* leaf, stem, and fruit biomass.

Statistical Analyses and Data Processing

We used the NLIN procedure in SAS 9.1.3 (SAS Institute 2000) to fit the Chapman-Richards function (Richards 1959, Sit & Poulin-Costello 1994) to the TAGB data. This allowed us to determine the rates and patterns of TAGB accumulation in secondary forests. We removed remnant standing trees and downed wood from our database prior to fitting the Chapman-Richards function. This prevented a confounding effect of remnant material on the size and accumulation patterns of TAGB pools. Excluding atypical sites > 20 yr in the Moist life zone improved the model fit considerably for that life zone. We used methods described by Olson (1963) and the parameter estimates from the fitted Chapman-Richards function to predict the age at which secondary forests reach TAGB levels equivalent to those in primary forests ($\geq 90\%$ TAGB). Mean annual increment (MAI) was calculated as the average of accumulated growth divided by age since pasture abandonment. Sites abandoned ≤ 1 yr were excluded from the analysis of MAI rates. The maximum MAI rates were calculated as the intercept of the regression curve of MAI vs. stand age.

The Chapman-Richards function has been successfully used to fit similar data from secondary forests of México and Brazil (Hughes *et al.* 1999, Neeff 2005, Vargas *et al.* 2008) and can accurately represent the cumulative growth pattern common in forested systems (Peng 1999, Colbert *et al.* 2002). This function estimates the aboveground biomass pools at time t as a sigmoid function that culminates at the maximum total

aboveground biomass recorded for a life zone (B_{\max} , measured in old-growth forests).

The function includes a biological accumulation rate-constant and an empirically-derived curvature parameter. The Chapman-Richards function can be expressed as:

$$B_t = B_{\max}[1 - \exp(-b_1 * t)]^{b_2} + \varepsilon \quad \text{where:}$$

- B_t is the total aboveground biomass for secondary forests ($\text{Mg} \cdot \text{ha}^{-1}$) at time t (years).
- B_{\max} is the asymptote of the curve, *i.e.* the maximum aboveground biomass ($\text{Mg} \cdot \text{ha}^{-1}$) fixed by forests in a life zone.
- b_1 is the shape parameter of the curve, *i.e.* the rate at which aboveground biomass approaches its maximum possible value (B_{\max}), which is related to the biological decay rate constant k ; $b_1 > 0$.
- b_2 is the inflection parameter of the curve, *i.e.* the “lag” commonly observed in early stages of secondary forest growth; $b_2 > 0$. When $b_2 = 1$ this function is equivalent to the natural growth function (Sit & Poulin-Costello 1994).
- t is the age of a secondary forest (years since agricultural abandonment).
- ε is the random error that adds variability to the value of B_t , $\varepsilon \sim N(0, \sigma^2)$ and is independent from other error terms in the model.

We assumed B_{\max} to be the average TAGB of primary forests measured previously in the same life zone (Kauffman & Hughes, in prep.). We used TAGB of Moist primary forests as reference for secondary forest TAGB accumulation in the Premontane Wet - Pacific life zone because of the similar physiognomy between primary forests in both life zones and the lack of TAGB data for Premontane Wet - Pacific primary forests. Data collected for pastures by a companion study (Jobse, unpublished data) served as minimum values for TAGB. We used the Marquardt iterative method to fit the Chapman-Richards function because of potential high correlation between the function's parameter estimates (Schabenberger & Pierce 2001). In addition, we used a range of initial values to ensure the solution for model parameters was global rather

than a local least-squares minimum. These initial values were based on published estimates of decomposition rate constants (k , Waring & Running 1998) and personal communications with other researchers (Mark Harmon and Flint Hughes personal communication). The default non-linear least-squares method was used because weighted regression did not produce improvements in model fit. We determined goodness of fit by calculating a “Pseudo- R^2 ” as described by Schabenberger & Pierce (2001).

To test the null hypothesis of no difference in function fits among life zones we used indicator variables and extra sums of squares (Peng *et al.* 2001). The appropriate test for the above hypothesis is an F-test (Neter *et al.* 1996, Schabenberger & Pierce 2001), where:

$$F^* = \frac{SSE_r - SSE_f}{df_r - df_f} \div \frac{SSE_f}{df_f}$$

with SSE= sum of squares of the error for full (_f) and reduced (_r) models, df_r = n-number of parameters in reduced model, and df_f = n-number of parameters in full model. The null hypothesis is rejected when $F^* > F_{\alpha; df_r, df_f}$. Significant differences ($\alpha = 0.05$) among life zones would support the interpretation that distinct biomass accumulation rates exist and as well as differences in maximum biomass pools between life zones. We used the overlap between 95% confidence intervals to assess differences between parameter estimates from different life zones. We assumed secondary forests characteristics were equivalent to those of primary forests when the

variables measured were $\geq 90\%$ of the corresponding values measured in primary forests (Hughes *et al.* 1999).

We tested the effect of assigning varying hypothetical ages to primary forests on our estimates of the time required by secondary forests to accumulate $\geq 90\%$ of the TAGB measured in primary forests. We assigned primary forests ages of 100, 200, 300, and 500 yr and fitted the Chapman-Richards using these alternative values. Parameter estimates for the Chapman-Richards function stabilized when primary forest age was ≥ 200 yr. When primary forest age was 100 yr, the parameter estimates for the Chapman-Richards function were equal to or $\leq 9\%$ smaller than those obtained when assuming primary forest age was ≥ 200 yr. We deemed this a small difference, given the potential errors associated with the quantification of TAGB (Chave *et al.* 2004), recent information on the successional status and potential age of primary forests (Clark 2007), and estimates of TAGB recovery elsewhere in the tropics (Ferreira & Prance 1999, Hughes *et al.* 1999, Read & Lawrance 2003, Saldarriaga *et al.* 1988, Vargas *et al.* 2008). We thus used 200 yr as a nominal primary forest age when fitting the Chapman-Richards function to our dataset.

We used ANOVA and the MIXED procedure in SAS 9.1.3 (SAS Institute 2000) to evaluate the significance of changes in the size of biomass pools with age, and to compare these between life zones. Variables were natural log-transformed and pooled into age categories when necessary to meet ANOVA assumptions (Read & Lawrance

2003). Pooling data by age categories provides a reasonable way of comparing change in ecosystem properties with time (Feldpausch *et al.* 2004). Least squares mean estimates and pair-wise differences between them were calculated using the LSMEANS routine in SAS 9.1.3 (SAS Institute 2000). We used the Tukey-Kramer method (SAS Institute 2000) to adjust the significance for multiple pair-wise comparisons.

To explore the relationship between environmental variables with B_{\max} and TAGB we used correlation analyses. We calculated Pearson correlation coefficients between B_{\max} , TAGB in secondary forests, temperature, precipitation, elevation, the ratio of potential evapotranspiration to precipitation (“PET ratio”, as described by Holdridge 1967), and secondary forest age. We used linear regression to test the relationship between TAGB and basal area of trees, lianas, and palms. Finding a strong linear relationship between TAGB and basal area would provide a simplified approach to quantifying TAGB in tropical forests growing on a diversity of climates without the need of performing detailed, time consuming, and expensive inventories such as the one presented here.

Results

Total Aboveground Biomass

There was a 25-fold difference in total aboveground biomass (TAGB) among the sampled secondary forests. TAGB in secondary forests ranged from 12 Mg·ha⁻¹ in a 9 yr Dry forest to 298 Mg·ha⁻¹ in a 60 yr Wet forest (Table 2.4). As expected, TAGB increased as secondary forests aged ($p < 0.0001$) and was significantly different among life zones ($p = 0.0141$). At similar ages, Drier life zones had lower TAGB than Wetter ones. TAGB in Dry secondary forests, for example, ranged between 12 Mg·ha⁻¹ in a 9 yr forest to 152 Mg·ha⁻¹ in a 27 yr forest. The latter represented 97% of the TAGB measured in Dry primary forests of the same life zone (Kauffman & Hughes in prep.) and demonstrates that Dry secondary forests sequestered biomass close to their maximum TAGB potential (*i.e.* TAGB values measured in primary forests) in a relatively short time. In contrast, we measured TAGB of 84 Mg·ha⁻¹ in a 9 yr Wet secondary forest, 246 Mg·ha⁻¹ in a 27 yr forest, and 298 Mg·ha⁻¹ in a 60 yr forest (Table 2.4). The latter represented 67% of the TAGB measured in primary forests in the Wet life zone (Kauffman & Hughes in prep.) and suggests secondary forests in the Wet life zone may require more time than those in the Dry life zone to reach TAGB comparable to that of primary forests.

Table 2.4. Total aboveground biomass (TAGB, Mg·ha⁻¹) partitioned by forest component in secondary forests of six life zones in Costa Rica.

Life Zone	Site	Age (yrs)	Wood debris	Surface layer	Palms	Lianas	Herba- ceous	Trees (dbh, cm)				Total	
								< 10	10-30	30-50	> 50	dead	TAGB
Tropical Dry	Pitahaya	9	0.0 ± 0.0	9.5 ± 1.7	0.0	0.1	0.0 ± 0.0	2.5 ± 1.3	0.1	0.0	0.0	0.0	12.2
	Bebedero	10	0.5 ± 0.3	9.5 ± 1.9	0.0	1.7	0.0 ± 0.0	16.9 ± 5.0	14.1	0.0	0.0	0.7	42.8
	Pocosol	10	0.0 ± 0.0	13.3 ± 2.5	0.0	0.1	0.0 ± 0.0	9.6 ± 6.5	10.1	0.0	0.0	0.0	33.1
	Mal Uso	14	1.6 ± 0.7	12.2 ± 2.3	0.0	2.9	0.0 ± 0.0	16.4 ± 4.0	17.8	0.0	0.0	2.1	51.4
	Deep Throat	16	0.4 ± 0.2	12.3 ± 2.4	0.0	6.7	0.0 ± 0.0	13.6 ± 4.4	31.8	1.5	0.0	1.3	67.2
	Firebreaks	17	0.3 ± 0.2	7.7 ± 1.3	0.0	0.0	0.0 ± 0.0	6.6 ± 2.9	6.9	0.0	0.0	0.3	21.5
	Príncipe	22	0.4 ± 0.2	14.9 ± 1.3	0.0	1.4	0.0 ± 0.0	22.6 ± 7.0	48.7	1.0	0.0	0.5	89.1
	Naranjo	26	11.7 ± 3.5	12.2 ± 3.4	0.0	3.2	0.0 ± 0.0	9.2 ± 1.8	35.2	51.6	0.0	13.9	125.4
	Buen Uso	27	6.8 ± 1.9	17.5 ± 5.1	0.0	7.6	0.0 ± 0.0	17.1 ± 2.1	79.6	22.6	0.0	7.3	151.7
	El Pozo	82	8.4 ± 3.1	9.8 ± 1.4	0.0	10.1	0.0 ± 0.0	5.3 ± 1.0	39.2	39.1	46.5	8.7	158.7
Tropical Moist	Downey	0.42	8.4 ± 3.4	9.6 ± 1.2	0.5	0.2	0.0 ± 0.0	2.0 ± 1.0	10.7	0.0	0.0	8.4	31.4
	Valle Azul	7	0.5 ± 0.2	6.8 ± 0.5	0.5	4.1	0.7 ± 0.4	6.2 ± 2.3	9.9	2.1	0.0	1.6	31.9
	Caballos	7	2.5 ± 0.6	7.8 ± 0.8	0.1	1.7	0.0 ± 0.0	12.0 ± 3.5	41.6	4.3	0.0	2.6	70.1
	Divino	9	1.6 ± 0.4	5.4 ± 0.9	0.0	12.7	0.0 ± 0.0	16.9 ± 4.4	33.1	0.0	0.0	2.1	70.2
	Iguana	13	1.5 ± 0.5	8.3 ± 0.8	4.7	7.3	0.1 ± 0.1	10.6 ± 4.6	63.6	0.0	0.0	1.7	96.3
	Quesera	16	4.2 ± 0.9	8.4 ± 0.6	0.0	5.2	0.0 ± 0.0	16.0 ± 4.3	76.1	2.1	0.0	9.1	116.9
	Dubya	20	2.0 ± 0.7	11.6 ± 1.9	9.5	5.1	0.0 ± 0.0	5.4 ± 2.1	47.0	0.0	0.0	3.2	81.7
	El Tanque	28	4.5 ± 0.9	7.4 ± 1.6	0.0	12.3	0.1 ± 0.1	7.8 ± 2.0	75.2	2.0	0.0	5.1	109.9
	Santa Teresa	30	3.6 ± 0.8	7.3 ± 0.8	0.7	0.9	0.8 ± 0.3	1.4 ± 0.5	53.6	9.3	0.0	5.7	79.6
	Chonco	40	3.4 ± 0.9	7.7 ± 1.0	1.6	5.1	0.0 ± 0.0	4.6 ± 1.5	61.2	6.4	0.0	3.5	90.2

Table 2.4. (Continued)

Life Zone	Site	Age (yrs)	Wood debris	Surface layer	Palms	Lianas	Herba- ceous	Trees (dbh, cm)				Total	
								< 10	10-30	30-50	> 50	dead	TAGB
Premontane Wet, Transition to Basal, Pacific	Yucal	2	1.7 ± 1.6	4.6 ± 0.9	0.0	1.0	0.0 ± 0.0	12.1 ± 2.0	1.4	0.0	0.0	2.2	21.3
	Chupadero	6	2.2 ± 1.0	5.9 ± 1.0	0.2	4.0	0.0 ± 0.0	8.4 ± 2.0	9.4	0.0	0.0	3.8	31.8
	Lapas	10	0.6 ± 0.2	3.4 ± 0.3	0.0	0.3	0.1 ± 0.1	5.2 ± 1.4	21.8	0.0	0.0	0.8	31.6
	Hotel	15	1.8 ± 0.6	8.2 ± 1.9	0.0	2.2	5.0 ± 3.5	4.5 ± 1.7	60.1	26.9	0.0	2.1	108.9
	Luciano	22	0.6 ± 0.2	5.8 ± 0.7	0.0	15.6	0.0 ± 0.0	16.9 ± 3.7	39.3	0.0	0.0	0.9	78.5
Premontane Wet, Transition to Basal, Atlantic	Cano	3	2.7 ± 0.9	7.7 ± 0.9	0.0	1.2	0.0 ± 0.0	8.6 ± 4.6	3.1	0.0	0.0	3.5	24.1
	SAT 900	6	2.0 ± 0.9	5.8 ± 1.1	0.0	4.2	0.3 ± 0.3	15.5 ± 4.1	14.4	0.0	0.0	2.1	42.3
	Con Permiso	10	23.0 ± 8.0	6.1 ± 1.2	0.3	2.5	0.0 ± 0.0	15.3 ± 2.1	38.7	3.9	0.0	24.3	91.2
	SAT 1000	15	10.8 ± 2.3	4.9 ± 0.9	0.2	9.2	0.0 ± 0.0	20.6 ± 2.8	32.1	11.8	0.0	11.4	90.3
	Pao	21	26.1 ± 4.7	6.4 ± 1.5	3.4	8.4	0.0 ± 0.0	9.7 ± 2.4	48.9	27.2	10.6	27.2	141.7
	Cascada	26	12.7 ± 3.2	5.0 ± 0.5	4.3	4.3	0.0 ± 0.0	12.1 ± 6.4	77.0	38.8	0.0	12.8	154.3
	Sábalo	27	26.7 ± 7.5	5.3 ± 0.7	1.7	4.3	0.0 ± 0.0	6.7 ± 1.7	38.6	71.8	45.0	26.9	200.4
	SHO 750	32	11.4 ± 4.0	4.6 ± 0.4	0.0	1.8	0.0 ± 0.0	10.4 ± 3.3	52.2	48.2	25.7	12.8	155.7
Tropical Wet	Terciopelo	0.7	0.8 ± 0.5	15.7 ± 1.6	0.0	0.1	0.0 ± 0.0	1.2 ± 0.5	0.0	0.0	0.0	0.9	17.9
	TUVA	1	2.7 ± 1.1	5.9 ± 0.9	0.0	1.1	0.0 ± 0.0	6.9 ± 1.2	1.0	0.0	0.0	3.2	18.1
	Culebra	3	6.3 ± 2.1	13.8 ± 1.8	0.0	10.3	0.0 ± 0.0	4.6 ± 1.9	7.2	0.0	0.0	6.3	42.2
	La Huerta	6.5	16.5 ± 3.7	6.2 ± 0.9	0.0	0.3	0.6 ± 0.2	6.9 ± 1.8	47.4	2.8	0.0	20.3	84.4
	Don Juan	9	10.9 ± 4.7	4.8 ± 0.9	1.0	2.2	0.0 ± 0.0	10.2 ± 2.1	55.1	0.0	0.0	11.0	84.3
	Tirimbina	18	16.8 ± 3.2	5.0 ± 0.5	0.2	10.8	0.0 ± 0.0	11.4 ± 3.6	69.2	3.3	0.0	18.8	118.8
	Piro	20	4.1 ± 0.8	4.5 ± 0.7	0.0	0.9	0.3 ± 0.1	10.9 ± 2.2	31.0	72.1	0.0	10.0	129.8
	Pumilio	25	29.3 ± 5.2	7.3 ± 1.0	2.0	4.4	0.0 ± 0.0	11.5 ± 2.7	75.4	6.3	0.0	30.0	136.8
	4 Ríos	29	5.6 ± 0.8	6.1 ± 0.8	5.1	3.2	0.0 ± 0.0	6.7 ± 2.6	108.2	109.8	0.0	7.1	246.2
	Caliente	35	12.1 ± 3.4	8.4 ± 1.1	1.1	2.9	0.0 ± 0.0	6.2 ± 2.3	61.1	61.1	19.0	12.1	172.1
	Palma Real	60	56.0 ± 27.0	4.9 ± 0.7	1.3	3.2	0.0 ± 0.0	12.0 ± 3.3	87.1	53.8	79.6	56.2	297.9

Table 2.4. (Continued)

Life Zone	Site	Age (yrs)	Wood debris	Surface layer	Palms	Lianas	Herba- ceous	Trees (dbh, cm)				Total	
								< 10	10-30	30-50	> 50	dead	TAGB
Premontane Rain	Volcán	0.5	3.1 ± 1.7	3.8 ± 2.2	0.0	3.2	0.0 ± 0.0	3.6 ± 1.4	3.4	0.0	0.0	3.1	17.1
	Vírgen María	10	5.7 ± 1.9	4.9 ± 0.7	1.1	3.0	0.0 ± 0.0	21.2 ± 6.8	43.8	0.0	0.0	6.4	80.5
	Alemán	15	3.0 ± 1.4	5.7 ± 0.6	0.9	3.0	2.8 ± 1.8	14.5 ± 4.9	73.8	2.2	0.0	3.5	106.3
	Cornelio	19	12.4 ± 4.0	5.3 ± 0.6	3.6	3.0	3.1 ± 1.6	14.2 ± 3.0	112.7	28.0	0.0	12.6	182.4
	Milpa	20	24.3 ± 5.8	7.5 ± 1.1	1.4	5.4	0.7 ± 0.4	8.4 ± 3.1	57.3	34.2	6.4	24.9	146.0
	Dos Ases	20	17.6 ± 4.0	8.5 ± 1.4	5.2	2.9	0.0 ± 0.0	9.0 ± 2.1	48.4	117.0	0.0	18.7	209.6
	Cambronerio	30	10.7 ± 2.7	8.1 ± 1.4	0.6	5.9	1.9 ± 1.2	7.6 ± 2.1	41.2	122.3	0.0	12.4	199.9
	Hondura	35	16.0 ± 4.1	12.6 ± 2.3	0.0	2.4	0.0 ± 0.0	9.4 ± 2.7	62.7	53.5	31.3	18.1	190.0
	Vargas	40	9.9 ± 2.5	7.1 ± 0.3	2.6	1.9	2.8 ± 1.9	9.5 ± 4.1	62.4	142.5	13.8	10.0	252.6
	Kraven S.A.	50	37.2 ± 9.6	6.9 ± 1.3	3.8	10.1	1.0 ± 1.0	15.1 ± 4.0	80.8	63.6	13.2	37.8	232.3

Notes: Mean ± SE is provided for ecosystem components sub-sampled within each 50 x 50 m plot, not for components that include whole plot measures. Surface layer includes litter and seedlings. Tree biomass is categorized by "diameter at breast height" (dbh) classes (cm); dbh was measured at 1.3 m height. Total dead includes wood debris, small dead stems dbh < 10 cm, and snags dbh > 10 cm. Total live includes all other categories. Total aboveground biomass (TAGB) is the sum of all aboveground biomass components.

Partitioning of Total Aboveground Biomass Among Forest Components

Live forest components such as trees, palms, and lianas, represented an average 91% of TAGB in all life zones. The average proportion of TAGB in live components was slightly higher (93 – 97%) in Drier forests than in Wetter ones (86 – 90%), but the difference was not significant ($p = 0.2235$). In contrast, Wetter life zones had greater amounts of aboveground dead biomass than Drier life zones ($p < 0.0001$, Table 2.4). Across life zones, aboveground biomass of live forest components was significantly smaller in secondary forests ≤ 20 yr than in secondary forests > 20 yr ($p < 0.0001$). In contrast, biomass of dead forest components was smallest in secondary forests ≤ 20 yr and increased with age (Table 2.4). In the Dry life zone, for example, total dead biomass was $2 \text{ Mg}\cdot\text{ha}^{-1}$ in a 4 yr secondary forest and $7 \text{ Mg}\cdot\text{ha}^{-1}$ in a 27 yr forest (Table 2.4). Total dead biomass was more abundant in the Wetter life zones. In the Premontane Wet - Atlantic life zone, for example, a 15 yr secondary forest had total dead biomass of $11 \text{ Mg}\cdot\text{ha}^{-1}$ and a 27 yr forest had total dead biomass of $27 \text{ Mg}\cdot\text{ha}^{-1}$ (Table 2.4). Despite this difference dead biomass represented $\sim 13\%$ of TAGB in both sites.

In all life zones, trees represented an increasing proportion of TAGB as secondary forests aged. For example, trees ranged between 7 and 91% of TAGB in Wet forests 0.7 to 29 yr (Table 2.4). Despite the high density of trees < 10 cm dbh in all life zones (Appendix B), the proportion of TAGB they represented decreased with secondary

forest age and did not exceed 4.5% of TAGB in secondary forests ≥ 30 yr (Table 2.4). Biomass of trees 10 – 30 cm dbh was positively related to forest age ($p = 0.0001$; Table 2.4). Biomass of trees 10 – 30 cm dbh was greatest in secondary forests 20 – 30 yr and smaller as succession continued and trees > 30 cm dbh became established (Table 2.4). For example, in Moist secondary forests, biomass of trees 10 – 30 cm dbh was $42 \text{ Mg}\cdot\text{ha}^{-1}$ in a 7 yr forest, $75 \text{ Mg}\cdot\text{ha}^{-1}$ in a 28 yr, and $61 \text{ Mg}\cdot\text{ha}^{-1}$ in a 40 yr forest (Table 2.4). A similar change was observed in the Wet life zone, where biomass of trees 10 – 30 cm dbh was $47 \text{ Mg}\cdot\text{ha}^{-1}$ in a 6.5 yr secondary forest, $108 \text{ Mg}\cdot\text{ha}^{-1}$ in a 29 yr forest, and $61 \text{ Mg}\cdot\text{ha}^{-1}$ in a 35 yr secondary forest. This represented a change in the proportion of TAGB in trees 10 – 30 cm dbh from 94 to 43% between the 6.5 and the 35 yr forests (Table 2.4). We did not find differences in biomass of trees 10 – 30 cm dbh between life zones ($p = 0.5340$).

Biomass of trees 30 – 50 cm dbh differed with age ($p < 0.0001$) but was not significantly different between life zones ($p = 0.2131$). In Premontane Wet - Atlantic secondary forests, biomass of trees 30 – 50 cm dbh was $4 \text{ Mg}\cdot\text{ha}^{-1}$ in a 10 yr forest and $72 \text{ Mg}\cdot\text{ha}^{-1}$ in a 27 yr forest. In comparison, TAGB of trees 30 – 50 cm dbh was 2 and $143 \text{ Mg}\cdot\text{ha}^{-1}$ in Premontane Rain secondary forests 15 and 40 yr (Table 2.4). Trees > 50 cm dbh were absent in Moist and Premontane Wet - Pacific secondary forests and were only present in a 82 yr Dry forest (Table 2.4), where they represented 29% of TAGB. This suggests it may take > 40 years for trees > 50 cm dbh to be evident in the Drier forests. However, once present, they compose a significant proportion of

TAGB. Trees > 50 cm dbh were also present in Wetter forests ≥ 20 yr, and represented a considerable proportion of TAGB as forests aged. For example, TAGB of trees > 50 cm dbh represented 22% of TAGB in a 27 yr Premontane Wet - Atlantic secondary forest, and 27% of TAGB in a 60 yr Wet secondary forest (Table 2.4). Overall, the proportion of larger diameter trees was largest in older secondary forests, which is consistent with generalized patterns of succession.

We did not find differences in surface litter biomass with secondary forest age ($p = 0.9770$), but the proportion of TAGB it represented was lower in all life zones as secondary forests increased in age (Table 2.4). For example, the proportion of surface layer biomass in Dry forests was 78% in a 9 yr forest and 12% in a 27 yr forest. In contrast, the proportion of surface layer biomass changed from 6 to 3% of TAGB between Premontane Rain forests 10 and 50 yr, respectively (Table 2.4). Dry and Moist life zones had greater amounts of surface layer biomass than the remaining life zones ($p < 0.0001$). Dry and Moist secondary forests had a mean surface layer biomass of 12 and 8 $\text{Mg}\cdot\text{ha}^{-1}$, respectively (Table 2.4). In contrast, Premontane Wet - Pacific and Atlantic forests averaged $\sim 6 \text{ Mg}\cdot\text{ha}^{-1}$.

In contrast to surface layer biomass pools, secondary forests in the Dry and Premontane Wet - Pacific life zones had lower downed woody debris than secondary forests in other life zones ($p < 0.0001$). Biomass of wood debris was 3 $\text{Mg}\cdot\text{ha}^{-1}$ in Dry secondary forests, which represented 3% of TAGB. Wood debris averaged 1.4 $\text{Mg}\cdot\text{ha}^{-1}$

in Premontane Wet - Pacific secondary forests, which represented 4% of TAGB. In comparison, wood debris biomass in Wetter forests averaged 14 – 15 Mg·ha⁻¹, which represented 9 – 13% of TAGB (Table 2.4). Biomass of downed wood increased with secondary forest age ($p=0.0031$). In the Wet life zone, for example, downed wood was 3 Mg·ha⁻¹ in a 1 yr and 56 Mg·ha⁻¹ in a 60 yr forest (Table 2.4).

Palms, lianas, and herbaceous vegetation were the smallest components of TAGB. The distribution of palms was very irregular across life zones. Palms were absent from Dry forests and most abundant in Moist secondary forests, where mature individuals of *Acrocomia* sp. are commonly left as remnants from forest to pasture conversion, or allowed to regenerate while the land was still being used for cattle grazing. The presence of palms was not related to secondary forest age (Table 2.4).

Lianas had the highest proportion of TAGB in Moist and Premontane Wet - Pacific forests (Table 2.4). However, we did not find differences in liana biomass between life zones ($p=0.2312$). The proportion of TAGB in lianas varied between secondary forests within a life zone. In the Moist life zone, the proportion of TAGB in lianas ranged from 1% (0.9 Mg·ha⁻¹) in a 30 yr forest to 18% (13 Mg·ha⁻¹) in a 9 yr forest. In the Premontane Wet – Pacific life zone, the proportion of TAGB in lianas ranged and from 1% (0.3 Mg·ha⁻¹) in a 10 yr forest to 20% (16 Mg·ha⁻¹) in a 22 yr forest, respectively (Table 2.4). Aboveground biomass of lianas ranged from 0 to 11 Mg·ha⁻¹ and represented 4 – 5% of TAGB in the remaining life zones. Across all life zones,

aboveground biomass in herbaceous vegetation did not exceed $5 \text{ Mg}\cdot\text{ha}^{-1}$. This represented an average 0.3% of TAGB (range: 0 – 4.6%) across all life zones (Table 2.4).

Patterns of TAGB Accumulation

Based on the TAGB pools measured in primary forests we classified the potential of secondary forests to accumulate TAGB into 3 distinct bioclimatic groups ($p = 0.0025$, Figure 2.5). Premontane Rain and Wet secondary forests had the highest maximum TAGB accumulation potential ($> 440 \text{ Mg}\cdot\text{ha}^{-1}$, Kauffman & Hughes in prep., Table 2.5). Moist, Premontane Wet - Pacific, and Premontane Wet - Atlantic secondary forests had an intermediate maximum TAGB potential ($262 - 285 \text{ Mg}\cdot\text{ha}^{-1}$, Kauffman & Hughes in prep., Figure 2.4). Finally, secondary forests in the Dry life zone had the lowest maximum TAGB accumulation potential among all life zones ($155 \text{ Mg}\cdot\text{ha}^{-1}$, Kauffman & Hughes, in prep., Table 2.5).

TAGB accumulation in Moist, Premontane Wet - Pacific and Atlantic, Wet, and Premontane Rain forests followed a natural growth pattern of accumulation (Table 2.5). TAGB pools increased rapidly in early stages of succession, had slower rates of TAGB accumulation in intermediate stages of succession, and reached a life zone-dependent TAGB asymptote as secondary forests aged (Figure 2.4). The TAGB accumulation pattern in Dry forests differed from all other life zones because the

phase of rapid secondary forest growth was preceded by a lag in TAGB accumulation in forests < 14 yr (Figure 2.4).

Maximum mean annual increment (MAI) rates of TAGB accumulation were 5.7 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in the Dry life zone and ranged between 8 and 11.4 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in the remaining life zones. Confidence limits around maximum increment rates overlapped, suggesting no significant differences among life zones. Mean annual rates of TAGB accumulation decreased with secondary forest age ($p=0.0069$). MAI rates of TAGB accumulation were 6.7, 5.8, and 5.5 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in secondary forests < 10, 10 – 20, and 20 – 30 yr, respectively. These values were not statistically different from each other ($p=0.4769 - 0.9838$). In contrast, the MAI rate of TAGB accumulation in secondary forests ≥ 30 yr was 3.5 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$; significantly lower than secondary forests < 10 and 10 – 20 yr ($p=0.0030, 0.0289$, respectively) but not significantly different from secondary forests 20 – 30 yr ($p=0.0855$).

We calculated Drier secondary forests would accumulate TAGB equivalent to that in primary forests in less time than Wetter forests. For example, Dry forests would reach $\geq 90\%$ of the TAGB present in primary forests in 35 years (Table 2.5). In comparison, Moist and Premontane Wet - Atlantic would take approximately twice that long to reach $\geq 90\%$ of the TAGB measured in primary forests. Furthermore, we calculated secondary forests growing in Wetter life zones would accumulate TAGB $\geq 90\%$ of the TAGB measured in primary forests in 108 to 124 yr (Table 2.5).

Total Aboveground Biomass

TAGB measured in Dry secondary forests < 10 yr was lower in our study than elsewhere in the tropics. For example, Read & Lawrance (2003) estimated TAGB of 10 to 18 Mg·ha⁻¹ in Dry Forests 3 yr in Yucatán, México. In addition, Vargas *et al.* (2008) measured TAGB of 37 Mg·ha⁻¹ in a 9 yr Dry forest in Quintana Roo, México. In contrast, TAGB in a 9 yr secondary forest in our study was 12 Mg·ha⁻¹ (Table 2.4). TAGB of secondary forests 10 – 20 yr in our study, however, were similar to those reported elsewhere. For example, Vargas *et al.* (2008) measured TAGB of 53 and 63 Mg·ha⁻¹ in secondary forests 14 and 15 yr, respectively. In comparison, we measured TAGB of 51 and 67 Mg·ha⁻¹ in secondary forests 14 and 16 yr, respectively. Once secondary forests were > 27 yr, TAGB in Costa Rica was ~ 2 times greater than that measured by Vargas *et al.* (2008), reaching a maximum of 159 Mg·ha⁻¹ in 82 yr after pasture abandonment (Table 2.4).

Table 2.5 Equations for predicting total aboveground biomass (TAGB, Mg·ha⁻¹) accumulation in secondary forests growing in six life zones of Costa Rica.

Life Zone	B _{max}	b ₁					Time to ≥ 90%
	(Mg·ha ⁻¹)	(yr ⁻¹)	b ₂	n	Pseudo-R ²		B _{max} (yrs)
Tropical Dry	154.8	0.1130 (0.0339)	5.1411 (3.1651)	11	0.95		35
Tropical Moist	262.1	0.0348 (0.0040)	1 --	7	0.95		66
Tropical Premontane Wet, Transition to Basal - Pacific	262.1	0.0214 (0.0041)	1 --	6	0.89		108
Tropical Premontane Wet, Transition to Basal - Atlantic	285.3	0.0316 (0.0025)	1 --	9	0.98		73
Tropical Wet	445.0	0.0186 (0.0015)	1 --	12	0.97		124
Premontane Rain	440.1	0.0202 (0.0016)	1 --	11	0.97		114

Notes: All equations are of the form $TAGB_t = B_{max} * [1 - \exp*(-b_1 * t)]^{b_2}$. TAGB_t is the TAGB (Mg·ha⁻¹) for secondary forest at time t (age of secondary forest, yr), B_{max} is the TAGB (Mg·ha⁻¹) measured in primary forests of a given life zone (Kauffman & Hughes in prep.), b₁ is the rate at which TAGB approaches B_{max}, b₂ is the inflexion parameter of the curve. The equation with b₁ and b₂ parameters is a Chapman-Richards function fit, whereas equations with only parameter b₁ are natural growth function fits. The standard errors of regression coefficients (SE) are in parentheses. Equation for Tropical Premontane Wet Transition to Basal Pacific life zone was statistically significant at $\alpha = 0.0015$. Equations for all other life zones were statistically significant at $\alpha < 0.0001$. Pseudo-R² calculated after Schabenberger & Pierce (2001). Time to ≥ 90% B_{max} = $-\ln(0.1)/b_1$ (Olson 1963).

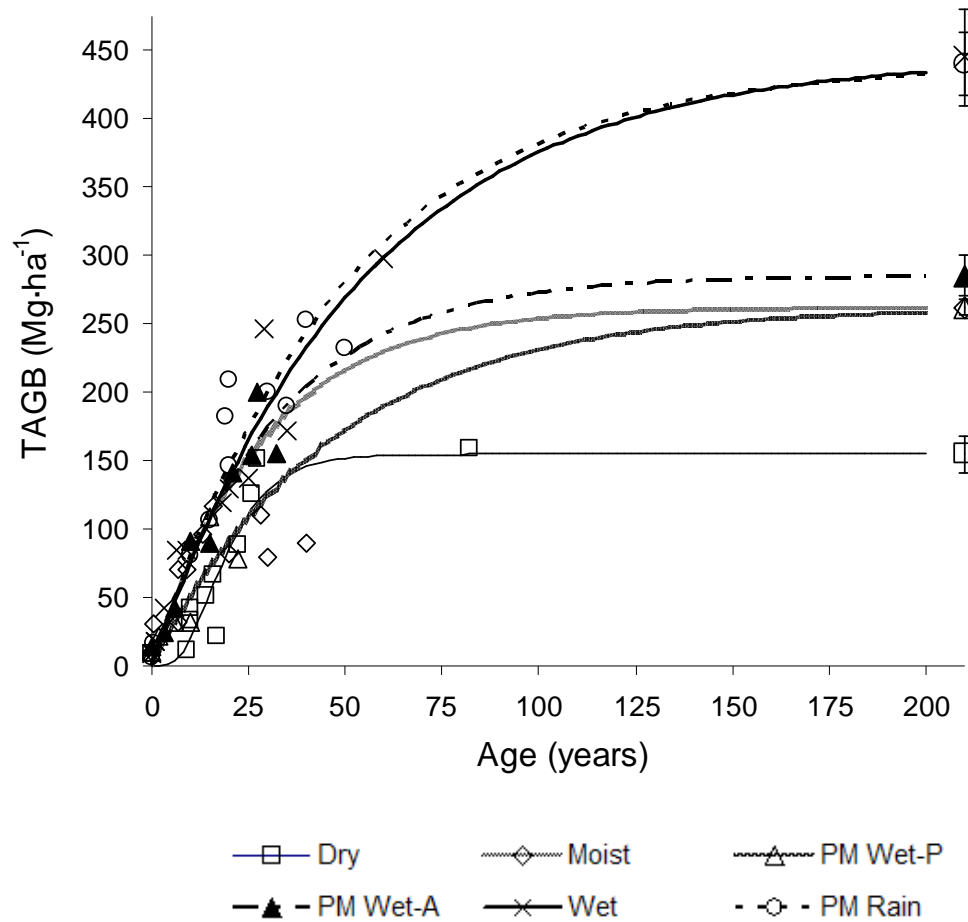


Figure 2.4 Accumulation of total aboveground biomass (TAGB, $\text{Mg}\cdot\text{ha}^{-1}$) with secondary age (years) in secondary forests growing in six life zones in Costa Rica. Points to the far right are the mean (\pm SE error bars) TAGB ($\text{Mg}\cdot\text{ha}^{-1}$) of primary forests in the corresponding life zones (Kauffman & Hughes in prep.). Secondary forests in the Dry life zone have low potential for TAGB accumulation, whereas forests in the Moist and Premontane Wet Transition to Basal life zones have intermediate TAGB accumulation potential. Forests in the Wet and Premontane Rain life zones have the highest TAGB accumulation potential. TAGB accumulation potential groups were significantly different from each other ($p=0.0025$). Curves represent growth functions fitted to the secondary forest TAGB data. Life zones are: Dry: Tropical Dry forest, Moist: Tropical Moist forest, PM Wet-P: Premontane Wet Transition to Basal - Pacific forest, PM Wet-A: Premontane Wet Transition to Basal - Atlantic forest, Wet: Tropical Wet forest, PM Rain: Premontane Rain forest.

Using Basal Area to Predict TAGB

We found a strong linear relationship between total basal area and TAGB ($R^2 = 0.89$, $p < 0.0001$). The relationship was stronger ($R^2 = 0.93$, $p < 0.0001$, Figure 2.3) when the regression was constrained to BA of trees, palms, and lianas ≥ 10 cm dbh (Appendix A). This suggests TAGB in tropical secondary forests may be predicted from stem diameter data without having to complete the exhaustive inventory of forest biomass presented in our study.

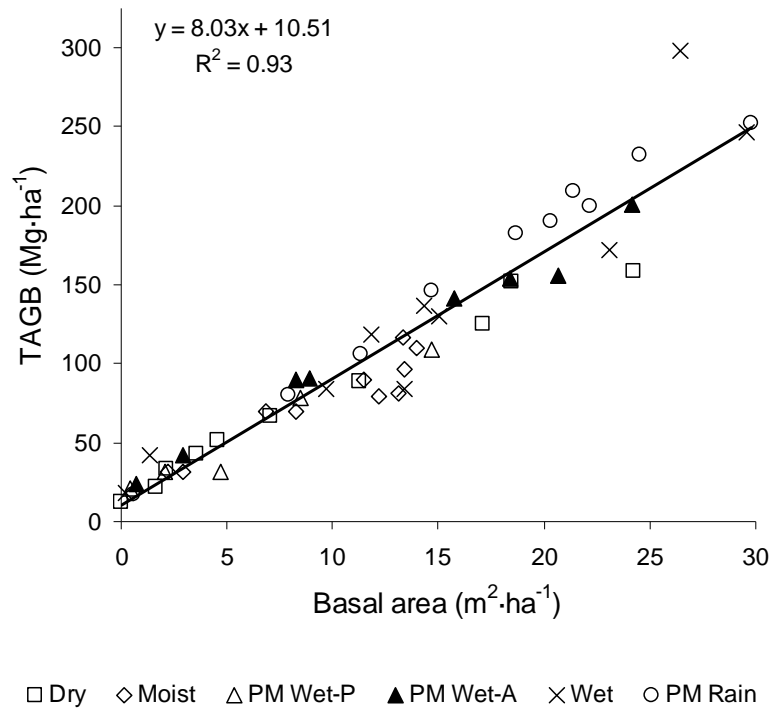


Figure 2.3. Linear relationship between basal area (m²·ha⁻¹) of trees, palms, and lianas ≥ 10 cm dbh and total aboveground biomass (TAGB, Mg·ha⁻¹) in secondary forests growing in six life zones of Costa Rica. Life zones are: Dry: Tropical Dry forest, Moist: Tropical Moist forest, PM Wet-P: Premontane Wet Transition to Basal forest - Pacific, PM Wet-A: Premontane Wet Transition to Basal forest - Atlantic, Wet: Tropical Wet forest, PM Rain: Premontane Rain forest.

Discussion

Total Aboveground Biomass

TAGB measured in Dry secondary forests < 10 yr was lower in our study than elsewhere in the tropics. For example, Read & Lawrance (2003) estimated TAGB of 10 to 18 Mg·ha⁻¹ in Dry Forests 3 yr in Yucatán, México. In addition, Vargas *et al.* (2008) measured TAGB of 37 Mg·ha⁻¹ in a 9 yr Dry forest in Quintana Roo, México. In contrast, TAGB in a 9 yr secondary forest in our study was 12 Mg·ha⁻¹ (Table 2.4). TAGB of secondary forests 10 – 20 yr in our study, however, were similar to those reported elsewhere. For example, Vargas *et al.* (2008) measured TAGB of 53 and 63 Mg·ha⁻¹ in secondary forests 14 and 15 yr, respectively. In comparison, we measured TAGB of 51 and 67 Mg·ha⁻¹ in secondary forests 14 and 16 yr, respectively. Once secondary forests were > 27 yr, TAGB in Costa Rica was ~ 2 times greater than that measured by Vargas *et al.* (2008), reaching a maximum of 159 Mg·ha⁻¹ in 82 yr after pasture abandonment (Table 2.4).

In a chronosequence of Moist secondary forests in the Rio Negro region, Colombia and Venezuela, Saldarriaga *et al.* (1988) reported TAGB increased from an average 75 Mg·ha⁻¹ in 9 – 14 yr secondary forests, to an average of 76 and 113 Mg·ha⁻¹ in 20 and 30 – 40 yr secondary forests, respectively. In the same study, they also measured an average 173 Mg·ha⁻¹ in 60 yr Moist secondary forests. These forests have lower

TAGB than Moist secondary forests elsewhere in the Neotropics (Alves *et al.* 1997, Fearnside & Guimarães 1996, Ferreira & Prance 1999, Steininger 2000, Uhl *et al.* 1988) because of the oligotrophic conditions in the study area (Denslow 2000). However, together with TAGB measured in sites degraded by intensive land use prior to the establishment of secondary forests (Fearnside & Guimarães 1996, Hughes *et al.* 2002), they are the most comparable to our data (Table 2.4). This suggests secondary forest growth in the Moist life zone of Costa Rica may be constrained by poor site conditions due to previous land use intensity.

Our TAGB estimates for Wet secondary forests ranged from 18 Mg·ha⁻¹ in a 1 yr forest, to 298 Mg·ha⁻¹ in a 60 yr forest (Table 2.4) and are comparable to other tropical Wet forests. In Wet secondary forests of Los Tuxtlas, México, Hughes *et al.* (1999) reported TAGB ranged between 5 and 287 Mg·ha⁻¹ between a recently abandoned pasture and a 50 yr secondary forest, respectively. Chacón *et al.* (2007) measured TAGB of 100 Mg·ha⁻¹ in a 20 yr Premontane Wet - Atlantic forests, while we measured 142 Mg·ha⁻¹ in a 21 yr forest in the same life zone. The lower TAGB reported by Chacón *et al.* (2007) is possibly due to their use of a simple volumetric equation with an expansion factor to calculate biomass of trees > 10 cm dbh. The use of different methods for calculating TAGB is an important source of uncertainty when comparing TAGB between different studies. The allometric equations we used to calculate TAGB (Table 2.3) have been shown to be a considerable improvement compared to alternative methods (Chave *et al.* 2004, Chave *et al.* 2005).

TAGB ranged from 17 to 200 Mg·ha⁻¹ in Premontane Rain secondary forests at ages 0.5 and 30 yr, respectively. The maximum TAGB for secondary forests in that life zone (253 Mg·ha⁻¹) was measured in a 40 yr forest. In comparison, Nadkarni *et al.* (2004) measured TAGB of 152 Mg·ha⁻¹ in a ~ 40 yr Lower Montane Moist secondary forest in Monteverde, Costa Rica. In addition, Fehse *et al.* (2002) reported TAGB in high elevation (2500 – 3600 m) Montane forests of Ecuador ranged between 177 and 206 Mg·ha⁻¹ in 30 yr forests. Although we cannot make direct comparisons between these different life zones, these data suggest Montane secondary forests across the tropics accumulate similar amounts of TAGB after 30 yr of secondary forest growth. Additional data from Montane secondary forests are needed to verify this suggestion.

Predicting TAGB Using Basal Area of Stems ≥ 10 cm dbh

TAGB can be predicted using data for basal area of stems > 10 cm dbh (Figure 2.3). Nightingale *et al.* (2008) also found a similar relationship across a series of old growth forests, plantations, and restoration sites of varying ages in humid tropical forests of Australia. While the slopes of the regressions were similar between our study and that reported by Nightingale *et al.* (2008) the intercept of the curve was higher in our study (analysis not shown). This suggests secondary forests in Costa Rica have higher TAGB than in Australia. In contrast, Cummings (1998) did not find a correlation between Brazilian forest structure variables (*i.e.* tree density and tree volume) from

primary forest inventories and actual TAGB. However, the dataset she used came from commercial timber inventories and included only trees ≥ 30 cm dbh and TAGB was calculated from tree volume through expansion factors. This may have limited the predictive power of the regression by introducing additional sources of error to the TAGB estimates (Chave *et al.* 2004).

It is possible that regions around the world may have different relationships between BA and TAGB. However, the consistency of the relationship between BA of stems ≥ 10 cm dbh (Appendix A) and TAGB (Table 2.4) observed between forests in Costa Rica and Australia (Nightingale *et al.* 2008), suggests TAGB can be predicted across a wide range of ages, basal area, and forest types using existing forest inventories that include data for stems ≥ 10 cm dbh.

Rates and Patterns of TAGB Accumulation

Consistent with other tropical studies (Brown & Lugo 1990, Guariguata & Ostertag 2001), the high TAGB accumulation rates we documented during early stages of succession decreased with increasing secondary forest age (Figure 2.5). The exception was the Premontane Wet - Pacific life zone, where MAI rates of TAGB accumulation did not follow a clear trend with secondary forest age (Table 2.4). This could be a reflection of the limited availability of sampling sites, coupled with undetermined differences in the sequence and intensity of previous land use in that life zone. The

latter has been shown to influence secondary forest recovery (Hughes *et al.* 1999, Uhl *et al.* 1988).

We did not find statistical differences in the maximum rates of TAGB accumulation between life zones. In addition, we found secondary forests < 30 yr had similar MAI rates of TAGB accumulation across life zones. Similarly, Brown and Lugo (1990) found mean growth rates were similar in secondary forests < 15 yr. Our results were also similar to findings by Silver *et al.* (2000), who found no effect of life zone on the rates of TAGB accumulation during the first 20 years of succession. Our data show Dry secondary forests have an extended period of establishment compared to other life zones (Figure 2.4). Once they become established, however, Dry forests have similar rates of aboveground biomass accumulation compared to those found in more humid forests, as predicted by Guariguata and Ostertag (2001).

We found similarities between our MAI rates of TAGB accumulation and those reported elsewhere for tropical secondary forests. For example, Vargas *et al.* (2008) found MAI rates ranged between 2.8 and 5.3 Mg·ha⁻¹·yr⁻¹ in a chronosequence of Dry secondary forests 4 to 29 yr. We calculated MAI rates between 1.3 to 5.6 Mg·ha⁻¹·yr⁻¹ in Dry secondary forests 9 to 27 yr (Table 2.4). Our estimates of MAI rates of TAGB accumulation for Moist secondary forests, ranging between 2.2 and 10 Mg·ha⁻¹·yr⁻¹, were lower than those reported for Moist forests in the Amazonian region (Alves *et al.* 1997, Fearnside & Guimarães 1996, Uhl *et al.* 1988, Saldarriaga *et al.* 1988). Hughes

et al. (1999) measured MAI rates of TAGB accumulation between 2.3 and 18.3 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in Mexican Wet secondary forests 0.5 to 50 yr (with no trend in MAI rates with secondary forest age). In turn, we estimated MAI rates between 4.9 and 18.1 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in Wet secondary forests 1 to 60 yr (Table 2.4). We also found similar MAI rates to those reported by Chacón *et al.* (2007) for a 15 yr Premontane Wet - Atlantic secondary forest ($\sim 6 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$). Finally, our estimates of MAI rates of TAGB accumulation in Premontane Rain secondary forests are at the lower end of the range reported by Fehse *et al.* (2002), but they sampled very productive, Montane Rain secondary forests in Ecuador.

Compared to a sigmoidal model (Richards 1959), the natural growth function best represented the pattern of TAGB accumulation in secondary forests growing in the Moist, Premontane Wet (Pacific and Atlantic), Wet, and Premontane Rain life zones. In contrast, secondary forests growing in the Dry life zone showed a lag early during succession and a sigmoidal function best represented TAGB accumulation with secondary forest age (Figure 2.5). This lag in early secondary forest growth possibly occurs because of the effect of seasonal water limitation on young vegetation (Ewel 1980, Murphy & Lugo 1986). Other factors that may explain this response include the absence of a seed bank due to a long and extensive land use history (Zimmerman *et al.* 2000) as well as repeated fires after pasture abandonment. In addition, isolation from currently available seed sources due to large scale deforestation in the region (Arroyo-Mora *et al.* 2005), absence of remnant vegetation (Guariguata & Ostertag 2001), and

increased seedling mortality due to low soil moisture may also be restricting forest establishment. Furthermore, the presence of this lag may be an artifact of our sampling since only Dry forests ≥ 9 yr were available for sampling. Despite this slow growth early in succession, the MAI rates of TAGB accumulation in Dry forests > 10 yr were comparable to that of other life zones (Table 2.4). It is possible that once a secondary forest becomes established in the Dry life zone, less competition for light between saplings, and access to deeper soil water may allow for increment rates comparable to those measured in other life zones. Overall, our results imply that, once established, secondary forests initially accumulate TAGB following similar patterns across a diversity of tropical climates. However, TAGB rates of accumulation vary as secondary forests age, and B_{\max} is different between life zones, which implies wetter life zones have higher TAGB accumulation potential than drier ones.

Time Required to Recover $\geq 90\%$ TAGB of Primary Forests

We originally predicted secondary forests in Wetter life zones would reach TAGB levels equivalent to primary forests in less time than Dry forests because they would accumulate more biomass per year. Instead, we did not find significant differences in the TAGB accumulation rates of secondary forests < 30 yr. Furthermore, we found secondary forests growing in Drier life zones reached TAGB equivalent to that in primary forests in a shorter time than secondary forests in Wetter life zones. The proportion of B_{\max} recovered with time (in our case, $\geq 90\%$) depends on the loss rate-

constant and is given by: $-\ln(0.1)/k$ (Olson 1963). Thus, life zones with higher loss rate constants (b_1 in Table 2.5) will reach their maximum pools faster. Dry secondary forests had the highest b_1 and reached TAGB equivalent to that in primary forests in 35 yr (Table 2.5). Conversely, Wet, Premontane Rain, and Premontane Wet - Pacific secondary forests had the lowest b_1 and their B_{\max} recovery periods exceeded 100 yr (Table 2.5).

We calculated that Dry forests would have the shortest B_{\max} recovery time of all life zones (Table 2.5). Predictions of TAGB recovery in other Dry forests are variable but greater than ours: 45 years in Subtropical Dry forests of Puerto Rico (Molina Colón & Lugo 2000), 80 years in Tropical Dry secondary forests of Quintana Roo, México (Vargas *et al.* 2008), and 55 – 120 years (dependent on the reference level of TAGB used) in Southern Yucatán, México (Read & Lawrance 2003). Dry secondary forests in Costa Rica recover TAGB equivalent to primary forests in shorter time periods than Dry forests elsewhere in the tropics likely because they are growing in more favorable conditions relative to Dry forests elsewhere in the tropics (Murphy & Lugo 1986).

We calculated it would require ~ 62 years to reach $\geq 90\%$ TAGB of primary forests in the Moist life zone (Table 2.5). Ferreira & Prance (1999) estimated 40 years was sufficient for secondary forests to attain 95% of TAGB pools measured in Moist primary forests of Brazil. However, this difference was greatly affected by the high proportion of trees > 60 cm dbh that were left standing after the original primary forest

was cleared for agriculture in the Brazilian sites. In contrast, Saldarriaga *et al.* (1988) estimated 189 years to recover biomass equivalent to that of a mature forest in the Rio Negro region of Colombia and Venezuela. These authors suggested very low soil fertility may be one reason for the long TAGB recovery time. In addition, the linear methods they used can overestimate TAGB recovery time.

Our estimates of TAGB recovery by Wet secondary forests are up to 4 times greater than those reported by Hughes *et al.* (1999) possibly because of slightly higher TAGB and lower biomass accumulation rates in our study. They calculated Wet secondary forests in Mexico would recover TAGC pools $\geq 90\%$ of those measured in primary forests in 31 to 79 yr after site abandonment, depending on the duration of previous land use. Longer and more intense land use practices that negatively affect soil properties and diminish rates of secondary forest growth and biomass accumulation (Fearnside & Guimarães 1996, Uhl *et al.* 1988) may explain why the expected time to recover TAGB is so much longer in Costa Rica. However, differences in soil types are also likely explanations for the differences between estimates. Hughes *et al.* (1999) sampled secondary forests growing on fertile Andisols, while most of the Wet secondary forests we sampled were growing on less fertile Ultisols (Table 2.2).

To further clarify general mechanisms controlling TAGB accumulation and determine how long it takes secondary forests to accumulate TAGB similar to that in primary forests, methodological issues must be resolved. Most studies cited here explicitly

state what level of recovery was considered equivalent to primary forest values (*i.e.* $\geq 90\%$ of primary forest TAGB). However, this is not always possible for tropical studies, where “equivalence” was not clearly defined (for example, Saldarriaga *et al.* 1988). In addition, a standardized approach for estimating time to primary forest recovery has not been agreed upon. Steininger (2000) and Saldarriaga *et al.* (1988), for example, used linear regression, while Hughes *et al.* (1999), Neeff (2005), and Vargas *et al.* (2008) used the same sigmoidal growth function (Richards 1959) as we did.

There are several methods for calculating standing biomass from diameter and height data, and the errors involved are not trivial (Chave *et al.* 2004). It is not always clear whether remnant trees were considered when calculating TAGB recovery in secondary forests. The presence of large remnant trees would significantly reduce the time required for secondary forests to recover TAGB similar to that measured in primary forest (Ferreira & Prance 1999). Some of these difficulties could be overcome by adopting standardized methods for estimating and monitoring TAGB in tropical secondary forests (Clark 2007). Despite the need for larger datasets, we suggest the allometric equations (Table 2.3) and the non-linear functions we used (Richards 1959, Sit & Paulin-Costello 1994) are most appropriate to represent secondary forest growth and obtain estimates of TAGB recovery. We also propose future studies consider using $\geq 90\%$ of primary forest TAGB as a measure of secondary forest recovery, or that they disclose what level of secondary forest TAGB is considered equivalent to that measured in primary forests.

Maximum Total Aboveground Biomass

The size of the TAGB pool in primary forests (B_{\max}) depends on the balance between rates of inputs and losses in the system (Chapin *et al.* 2002), which are influenced by a multitude of environmental factors (soils, water availability, temperature, etc.).

Accordingly, B_{\max} can be determined by the ratio of production, I , to a fractional loss rate, k (b_1 in Table 2.5, Olson 1963). Small values of k relative to values of I result in higher maximum TAGB, and vice versa. For example, in the Premontane Rain life zone $k = 0.0202 \text{ yr}^{-1}$ and $I = 8.9 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$, while in the Moist life zone $k = 0.0348 \text{ yr}^{-1}$ and $I = 9.1 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Table 2.5). In the latter life zone B_{\max} was $445 \text{ Mg} \cdot \text{ha}^{-1}$, while in the former it was $262 \text{ Mg} \cdot \text{ha}^{-1}$ (Table 2.5).

Consistent with expectation (Murphy & Lugo 1986, Silver *et al.* 2000), B_{\max} was greater in life zones with greater precipitation. The amount of TAGB potentially accumulated by Wet and Premontane Rain secondary forests is 3 times greater than that in Dry secondary forests and 1.5 – 1.7 times greater than that in Moist and Premontane Wet secondary forests (Figure 2.5). We found B_{\max} was positively correlated to mean annual precipitation ($r^2 = 0.90$, $p = 0.0361$) and negatively correlated ($r^2 = -0.90$, $p = 0.0421$) to the “PET Ratio” described by Holdridge (1967). In secondary forests, the size of TAGB pools was strongly correlated to age ($r^2 = 0.75$, $p < 0.0001$). In addition, a linear combination of age since pasture abandonment and

PET Ratio or mean annual precipitation best explained the size of TAGB pools ($R^2 = 0.76$, $p < 0.0001$) in secondary forests. This suggests a combination of water availability, temperature, and age affects secondary forest growth and ultimately B_{\max} , through its influence on nutrient and oxygen availability in the soil, increment and decomposition rates for any life zone (Johnson *et al.* 2000, Raich *et al.* 2006, Schuur 2003). These relationships could be used for understanding differences in TAGB pool size and shifts in TAGB accumulation rates in tropical forests under changing climatic conditions.

We suggest differences in maximum TAGB pools between life zones may be partially due to water availability and temperature indirectly affecting ecosystem processes. Thus, in the context of accumulating the largest amounts of TAGB, efforts could be focused on promoting secondary forest growth in Wetter life zones. With ongoing climate change, however, careful consideration should be devoted to where TAGB accumulation should be preferentially carried out and whether the expected target for recovery based on past growth rates is realistic for the future (Harris *et al.* 2006). For example, climate change models for Costa Rica predict an increase in temperature of up to 4.5 °C and a generalized but spatially heterogeneous reduction of precipitation across the country with a doubling of pre-industrial atmospheric CO₂ concentrations by the year 2075 (Campos 1999). This would eliminate the area of Premontane Rain forest and reduce the area of Tropical Wet life zones across the country, while increasing the extent of Premontane Wet Transition to Basal life zones (MINAE/IMN

1996). Thus, while we calculated secondary forests growing in the Premontane Rain and Tropical Wet life zones currently have the potential to accumulate 190 – 200 $\text{Mg}\cdot\text{ha}^{-1}$ in 30 years (Figure 2.4), and are expected to recover $\geq 90\%$ of the TAGB of primary forests in 114 – 124 yr, future climatic conditions may impede attaining that potential. In the long term, establishing secondary forests in the Premontane Wet - Atlantic life zone may be most promising for accumulating TAGB. Secondary forests growing in this life zone have considerable potential to accumulate TAGB (175 $\text{Mg}\cdot\text{ha}^{-1}$ in 30 yr, Figure 2.4). In addition, they are expected to recover B_{max} in 73 yr, and the area of the life zone is predicted increase with future climate change (MINAE/IMN 1996). However, the effect of future climate conditions and the shift in life zones from higher to lower B_{max} on biomass and C dynamics remains to be determined. This highlights the importance of quantifying current TAGB pools in secondary forests across a range of climatic conditions to strengthen our ability to predict future TAGB accumulation in a changing world.

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CHAPTER 3

TOTAL ECOSYSTEM CARBON IN TROPICAL SECONDARY FORESTS GROWING IN SIX LIFE ZONES OF COSTA RICA

Abstract

Tropical forests play very important roles in the global C cycle. To adequately manage adaptation and mitigation strategies for global climate change, the amount of C sequestered by secondary forests growing in different climates must be known. Total ecosystem carbon was measured in 54 secondary forests occurring six life zones in Costa Rica. About 30 years after pasture abandonment, total aboveground carbon (TAGC) accumulation reached 93 to 118 Mg·ha⁻¹ in the Premontane Rain and Wet life zones, and 37 to 70 Mg·ha⁻¹ in the Moist and Dry life zones. Secondary forests were predicted to reach TAGC \geq 90% of that in primary forest in 116 to 126 yr in the Premontane Rain and Wet life zones, and 35 to 67 yr in the Dry and Moist life zones, respectively. Soil C pools to 1 m depth ranged between 118 and 127 Mg·ha⁻¹ in the Dry, Premontane Wet - Pacific and Moist life zones, and between 157 and 278 Mg·ha⁻¹ in the Wet, Premontane Wet - Atlantic, and Premontane Rain life zones. Time since agricultural abandonment was not a good predictor of the size of soil C pools for any of the life zones. TEC sequestration was largely a function of aboveground C accumulation. Total ecosystem C pools (above and below ground C) were greater in the Wet, Premontane Wet - Atlantic, and Premontane Rain life zones (229 - 370 Mg·ha⁻¹) than in the Dry, Premontane Wet - Pacific, and Moist life zones (149 - 171 Mg·ha⁻¹). Secondary forests were predicted to attain ecosystem C levels \geq 90% of those measured in primary forests in 44 to 105 years of succession. Maximum rates of total ecosystem C accumulation were highest (14 – 33 Mg·ha⁻¹·yr⁻¹) in life zones with

intermediate levels of precipitation and lowest in the Dry and Premontane Rain life zones (7 and 12 Mg·ha⁻¹·yr⁻¹). The differing rates of sequestration by life zone could suggest how climate change to new levels of precipitation and temperature may affect the potential for secondary forests to accumulate C in the future.

Introduction

Secondary forests are an increasingly important component of tropical landscapes because of their large areal extent and fast growth rates (Brown and Lugo 1990). Emrich *et al.* (2000) estimated secondary forests represent 35% of all tropical forests in the world. In tropical America, it is estimated secondary forests cover at least 335 million hectares (FAO 2005), and it is suggested they are becoming the prevailing type of forests in many tropical regions, even exceeding the area covered by primary forests in some countries (FAO 2005, Wright & Mueller-Landau 2006). In Costa Rica, for example, secondary forests are estimated to cover similar area than primary forests (~25% of the country, Kleinn *et al.* 2005). Secondary forests play an important role in sequestering C (Silver *et al.* 2000a, Wright & Mueller-Landau 2006). Niles *et al.* (2002), for example, estimated regenerating forests globally have the potential to accumulate 316 Tg of C over a 10 year period, with 56% of that potential coming from Latin American countries. This is equivalent to 69% of the C emitted from tropical deforestation in the 1990s (DeFries *et al.* 2002).

Considerable attention has been given to quantifying carbon pools in primary tropical forests (Clark 2002, Clark 2004, Delaney *et al.* 1997, Hughes *et al.* 2000, Hughes *et al.* 2002, Jaramillo *et al.* 2003) and, more recently, secondary forests (Fearnside & Guimarães 1996, Hughes *et al.* 1999, Feldpausch *et al.* 2004, Sierra *et al.* 2007, Vargas *et al.* 2008). However, secondary forest research has generally focused on humid and wet lowland climates (Brown & Lugo 1990, Finegan 1996, Finegan & Delgado 2000, Guariguata & Ostertag 2001, Saldarriaga *et al.* 1988). In addition, soil investigations have been generally limited to shallow soil depths (Buschbacher *et al.* 1988, Chacón *et al.* 2007, Vargas *et al.* 2008), although it has been documented that deep roots may play an important role in the C cycle (Nepstad *et al.* 1994). Multiple studies have separately quantified aboveground and soil C pools in tropical ecosystems, but assessments of total ecosystem carbon storage and change of that storage done over time in different life zones and with the same methods are extremely limited (Clark 2004, Hughes *et al.* 1999, Vargas *et al.* 2008).

One of the major uncertainties concerning the role of tropical forests in the global carbon cycle is the lack of adequate data on the C mass and rates of sequestration of all their components (Delaney 1997, Clark *et al.* 2001). This research is the first to provide such baseline data on changes in above and below ground C pools for secondary forest chronosequences growing in a diversity of tropical climates (*i.e.* life zones, *sensu* Holdridge 1967). The main objective of this study was to characterize the

total above and below ground C pools to 1 m depth (including C in mineral soil and in roots) of secondary forests growing in six life zones in Costa Rica. In addition, we aimed to describe the rates of C sequestration and the time required for secondary forests to attain total ecosystem C equivalent to that in primary forests. We assumed that, given enough time, secondary forest ecosystem C pools would be equivalent to those of primary forests. In addition, we hypothesized ecosystem C pools would be larger and sequestration rates faster in wetter climates.

Methods

Site selection

We sampled 54 secondary forests of varying ages in 6 life zones (Holdridge 1967) of Costa Rica (Table 2.2): Tropical Dry forest, Tropical Moist forest, Premontane Wet Transition to Basal forest (Atlantic and Pacific rainfall regimes were considered separately because of forest physiognomy differs among these regimes), Tropical Wet forest, and Premontane Rain forest. For the purposes of this research, we refer to these life zones as Dry, Moist, Premontane Wet - Pacific, Premontane Wet - Atlantic, Wet, and Premontane Rain. Also, we refer to the first three life zones as “Drier” because of the occurrence of a distinct dry season (when monthly rainfall is < 100 mm), and the remaining as “Wetter” (rainfall > 100 mm year-round). Together, these life zones

represent approximately 55% of the country (Bolaños & Watson 1993) and form a bioclimatic gradient from warm and dry to cool and wet forests.

Secondary forests in each life zone were located by overlaying the 1:200 000 Life Zone System Map for Costa Rica (Bolaños and Watson 1993) with the 1992 Land Use Map (MAG 1992) in a GIS. Once sites were located, we interviewed local residents to verify the range of secondary forest ages available for sampling within a life zone. Only sites previously used as pastures (the most common agricultural use) were chosen. Secondary forests subject to logging or other silvicultural operations were not considered. Also, patches of secondary forests had to be ≥ 1.5 times larger than our plot size (0.25 ha).

Chronosequences spanning the age range of secondary forests within each life zone were sampled. Each chronosequence included secondary forest stands in different geographic regions of the country. The exception was the Tropical Dry forest life zone because it is restricted to a single geographic region of Costa Rica. We sampled one Premontane Wet life zone chronosequence in the Atlantic, and one in the Pacific regions of Costa Rica (Chapter 2, Table 2.2). Although both areas are classified as the same life zone (Holdridge 1967), the Pacific region of Costa Rica has a distinct Dry season leading to different physiognomies than in Premontane Wet - Atlantic forests (Holdridge *et al.* 1971).

Ecosystem C pools

We defined ecosystem C pools as the sum of all organically-derived C present in mineral soils, roots, and aboveground forest components. We used methods similar to those described by Hughes *et al.* (1999) to quantify aboveground and soil C pools. In addition, we calculated the amount of C allocated to roots based on TAGC (Table 3.2) using equations developed by Cairns *et al.* (1997) and assuming roots have 49% C content (Jackson *et al.* 1997). We did not quantify the C pool of epiphytes because they represent only ~ 0.1% of total ecosystem C pools in secondary forests (Nadkarni *et al.* 2004).

We sampled all aboveground ecosystem components and soils in a 50 x 50 m (2500 m²) nested plot (Figure 3.1). This plot size provides an appropriate sampling area for large trees and is of adequate size to describe successional trajectories (Chave *et al.* 2004, Hughes *et al.* 1999, Saldarriaga 1998). In all plots, the diameters at breast height (dbh, measured at 1.30 m height, Philips & Baker 2002) of all trees, palms, and lianas ≥ 10 cm dbh rooted within the 50 x 50 m plots were measured. In addition, the mass of dead trees and palms was calculated from measurements of both dbh and height of each snag; the latter obtained with a clinometer. The diameter and height of all stumps were also measured inside the main plot. The species, growth form (*e.g.* tree, liana/vine, palm, snag), and whether the stem was dead or alive, were also recorded. We used species names and live/dead status to assign the appropriate wood specific

gravity data for biomass calculations (Chapter 2, Table 2.3). Samples from plants not identified to species in the field were taken to the Tropical Science Center or the Instituto Nacional de Biodiversidad (InBio) for identification.

We measured the diameter of all trees < 10 cm dbh and taller than 1.30 m inside eight 1 x 15 m subplots at each sampled site. These small tree subplots were located on the periphery of the main plot and randomly oriented ($n= 8$; Figure 3.1). Live stems < 1.30 m in height (saplings) were considered part of the forest floor and collected in eight 0.5 x 0.5 m microplots adjacent to each small tree subplot and located 2 m away from the subplot's origin ($n= 8$). We also collected dead saplings, seedlings, and all downed material (litter) found inside this microplot (Figure 3.1). Surface litter was composed of leaves, bark fragments, seeds, flowers, fruits, and small woody stems ≤ 2.54 cm in diameter. Downed wood (*i.e.* dead wood material with diameter > 2.54 cm) was measured along two 15 m, randomly oriented, transects located at 8 points in the periphery of the plot ($n= 16$, Figure 3.1) using the planar intersect technique (Brown & Roussopoulos 1974, Van Wagner 1968). Plant tissue samples representative of all these ecosystem components were collected to determine C concentrations (Table 3.1).

Dry mass of each ecosystem component was calculated using a combination of life zone-specific allometric equations developed specifically for each ecosystem component or determined directly from oven-dried field samples (Chapter 2, Table

2.3). Aboveground C pools were calculated by multiplying the mass of each ecosystem component by its corresponding C concentration (Hughes *et al.* 1999). We used C concentrations from tissue samples previously collected for each biomass component (Hughes *et al.* 1999; Kauffman & Hughes in prep.), or collected specifically for this study (Table 3.1). All plant tissue and soil samples were oven-dried to constant mass at 65 °C and then ground to pass through a 0.5 mm mesh. Soil samples were sieved to remove roots, rocks, and debris > 2 mm in diameter and ground to pass through a 250 µm pore size.

To determine the C pools of mineral soils we collected samples at 10 m intervals along a 50 m transect established in the center of each 50 x 50 m plot (Figure 3.1). At each of the five sampling points along the 50 m transect, samples were obtained by compositing four subsamples collected 1 m from the sampling point in each cardinal direction. Soils were collected from 0 – 10, 10 – 20, 20 – 30, 30 – 50, and 50 – 100 cm depths (n= 25; 5 sampling locations x 5 depths per plot). Bulk density was determined by weighing 5 samples of known volume extracted from the mid-point for each of these depth intervals (Anderson & Ingram 1993). All soil samples were obtained with an Eijkelkamp soil core sampler (Eijkelkamp Agriresearch Equipment, The Netherlands). All tissue and soil samples were analyzed at the Habitat Ecology Laboratory, Department of Fisheries and Wildlife, Oregon State University. Carbon concentrations in biomass and soils were determined by the induction furnace method in a Carlo-Erba NA Series 1500 NCS analyzer (Nelson and Sommers 1996).

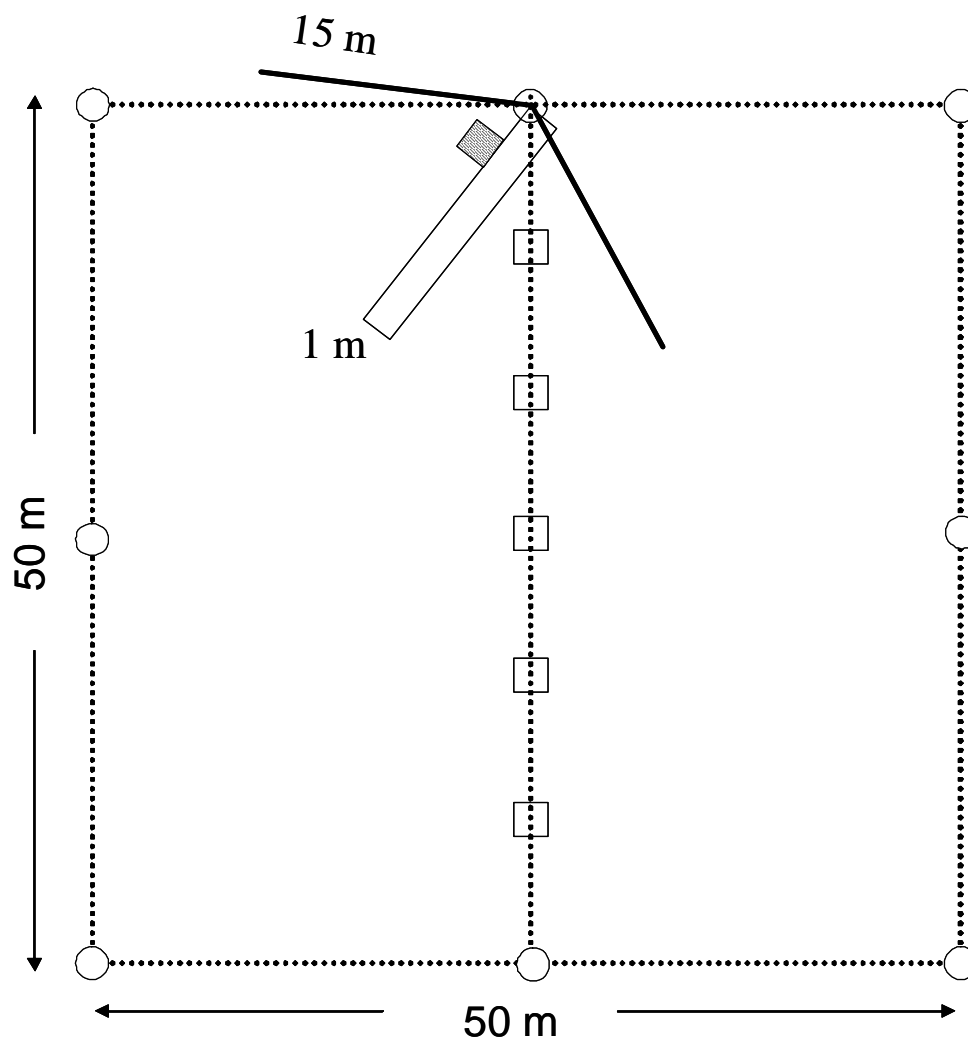


Figure 3.1. Plot layout to quantify mass of ecosystem carbon ($\text{Mg}\cdot\text{ha}^{-1}$) in secondary forests of six life zones in Costa Rica. The plot perimeter and the center line of the plot are shown in dotted lines. Soil sampling areas (open squares) were spaced 10 m from each other along the center line of the plot. Although only a pair of random-direction downed wood transects (solid lines) and small tree subplots (open rectangle) is represented here, a similar pair originated at all locations marked with open circles ($n=16$ downed wood transects, $n=8$ small tree subplots). A forest floor microplot (striped square) was associated with each small tree subplot ($n=8$).

Table 3.1 Concentration of C (% , mean \pm SE) in components of aboveground vegetation in secondary forests of six life zones in Costa Rica.

Vegetation Component	Life Zone				
	Tropical Dry	Tropical Moist	PM Wet	Tropical Wet	PM Rain
Leaves	45.46 \pm 0.04	46.48 \pm 0.08	44.52 \pm 0.04	45.36 \pm 0.12	46.49 \pm 0.04
Litter	40.81 \pm 0.15	43.79 \pm 0.14	44.01 \pm 0.16	44.42 \pm 0.15	47.60 \pm 0.31
Lianas & Herbaceous	46.85 \pm 0.19	46.28 \pm 0.12	45.84 \pm 1.03	46.68 \pm 0.19	47.27 \pm 0.26
Palm Leaves	45.25 \pm 0.06	45.59 \pm 0.14	45.22 \pm 0.09	46.34 \pm 0.02	45.46 \pm 0.07
Palm Stems	50.85 \pm 0.03	47.12 \pm 0.02	47.88 \pm 0.05	48.16 \pm 0.01	43.60 \pm 0.03
Rotten Wood	47.19 \pm 0.10	45.98 \pm 0.07	47.49 \pm 0.10	49.08 \pm 0.09	48.07 \pm 0.05
Sound Wood	48.05 \pm 0.12	47.90 \pm 0.03	48.76 \pm 0.01	48.69 \pm 0.24	47.97 \pm 0.05

Note: PM Wet: Premontane Wet Transition to Basal – Pacific forest, PM rain: Premontane Rain forest. Litter C concentration (% , mean \pm SE) in the Premontane Wet Transition to Basal – Atlantic life zone was 46.36 \pm 0.17. No other samples were available for that life zone.

Soil C pools partitioned by depth were determined by multiplying soil C concentrations by the bulk density of each depth layer and the corresponding layer thickness. We accounted for the influence of compaction on estimates of soil C by using the “equivalent mass” approach described by Ellert & Bettany (1995). This required the determination of soil mass to a given depth in soils of primary forests and using that mass as a standard to calculate the equivalent soil sampling depth (Ayanaba 1976) in secondary forests. The adjusted soil C pools in secondary forests were then obtained by summing the mass of C stored in successive soil layers that contained mass of soil equivalent to that measured to 1 m depth in primary forests. By doing this, we avoided potentially overestimating the total soil C content (Ellert 1995, Ellert *et al.* 2001), by an average of 13%, because of differences in bulk density between contrasting land use types.

Rates of Ecosystem Carbon Sequestration

To describe the rates of sequestration and the time required for secondary forests to attain ecosystem C equivalent to that measured in primary forests we fitted the natural growth function (Sit & Poulin-Costello 1994) to predicted ecosystem C data using the NLIN procedure in SAS 9.1.3 (SAS Institute 2000, Chapter 2). We assumed secondary forests would be equivalent to primary forests when they attained $\geq 90\%$ of the ecosystem C of primary forests (Kauffman & Hughes in prep.). Predicted ecosystem C sequestration data consisted of the sum of TAGC measured in the field, and root C and soil C calculated using regression equations (Cairns *et al.* 1997, Silver *et al.* 2000a). Available equations for predicting soil C are limited to 25 cm depth (Silver *et al.* 200a). To control for the confounding effect of remnant aboveground material on C sequestration rates we excluded remnant standing trees and downed wood from TAGC. We did not use our field measurements of soil C because their high variability prevented us from detecting changes with forest age.

We used methods described by Olson (1963) and the parameter estimates from the fitted natural growth functions of each life zone to predict the age at which secondary forests would reach ecosystem C levels $\geq 90\%$ to those measured in primary forests. Mean annual ecosystem C sequestration rates were calculated as the average of predicted ecosystem C divided by the secondary forest age. Maximum mean annual C sequestration rates were calculated as the intercept of a negative exponential

regression curve between mean annual ecosystem C sequestration rates and secondary forest age. We excluded sites ≤ 1 yr from the analysis of mean annual sequestration rates because of spurious data.

Statistical Analyses and Data Processing

We used ANOVA and the MIXED procedure in SAS 9.1.3 (SAS Institute 2000) to evaluate the significance of changes in TEC and MAI rates with forest age, and make comparisons between life zones. Variables were natural log-transformed, and pooled into age categories when necessary, to stabilize the variance and meet other ANOVA assumptions (Read & Lawrence 2003). Pooling data by age categories provides a reasonable way of comparing change in ecosystem properties with time (Feldpausch *et al.* 2004). Least squares mean estimates and pair-wise differences between them were calculated using the LSMEANS routine in SAS 9.1.3 (SAS Institute 2000). We used the Tukey-Kramer method (SAS Institute 2000) to adjust the significance for multiple pair-wise comparisons. We used correlation to determine the strength of the relationship between TAGC, soil C, and ecosystem C with forest age, temperature, precipitation, and elevation.

Results

Total Aboveground Carbon Pools

Total aboveground carbon (TAGC) pools were highly variable in secondary forests, ranging from 5 Mg·ha⁻¹ in a 9 yr Dry forest to 143 Mg·ha⁻¹ in a 60 yr Wet forest (Table 3.2). As expected, we found an increase in the size of TAGC pools with age across all life zones ($p = 0.0049$). At any given age TAGC was, in general, greater in Wetter life zones than in Drier ones (Table 3.2). TAGC was correlated ($r^2 = -0.3813$, $p = 0.0044$) with the ratio of potential evapotranspiration to precipitation (*i.e.* an index of available moisture, Holdridge 1967). Live forest components such as trees, palms, and lianas represented 86 to 97% of TAGC (Table 3.2). In all life zones, TAGC followed a non-linear pattern of sequestration with secondary forest age. In most life zones this pattern was characterized by very rapid growth early in succession, decreasing accumulation rates in mid-succession, and a slow approach to a maximum TAGC similar to that in primary forests (Chapter 2).

Secondary forests attained TAGC levels $\geq 90\%$ of those in primary forests at different ages after pasture abandonment. Dry secondary forests reached TAGC levels equivalent to those in primary forests (73 Mg·ha⁻¹, Kauffman & Hughes in prep.) in 35 yr after pasture abandonment. In the Moist, Premontane Wet - Atlantic, and Premontane Wet - Pacific life zones, secondary forests attained TAGC levels

equivalent to those in primary forests ($123 - 138 \text{ Mg}\cdot\text{ha}^{-1}$, Kauffman & Hughes in prep.) in 67, 76, and 110 yr following pasture abandonment, respectively. We predicted Premontane Rain and Wet secondary forests would reach TAGC levels $\geq 90\%$ of primary forests ($207 - 215 \text{ Mg}\cdot\text{ha}^{-1}$, Kauffman & Hughes in prep.) in 116 and 126 yr after pasture abandonment, respectively.

Characterization of Soil Carbon Pools.

Soil Carbon Concentration

We did not find differences in soil C concentration with forest age ($p = 0.1311$). However, we found significant differences in soil C concentrations between life zones ($p < 0.0001$). In addition, soil C concentrations decreased with depth ($p < 0.0001$). At all depths, soils of Premontane Rain forests had the highest mean soil C concentration (Figure 3.4). Differences among life zones were most apparent at the soil surface and decreased with increasing soil depth (Figure 3.4). In the 0 – 10 cm depth layer, for example, mean soil C concentration in Premontane Rain forests was approximately 16.4%, or 4 – 6 times greater than in the Dry, Moist, or Premontane Wet - Pacific life zones (3.8, 3.4, and 2.7%, respectively), and ~ 3 times greater than in the Premontane Wet - Atlantic and Wet life zones (5.6 and 5.1%, respectively, Figure 3.4). This difference persisted with depth; soil C concentration at the 50 – 100 cm depth layer in Premontane Rain forests was 3 – 5 times greater than in the Dry, Moist, or Premontane

Wet - Pacific life zones, and ~ 3 times greater than in the Premontane Wet - Atlantic and Wet life zones (Figure 3.4).

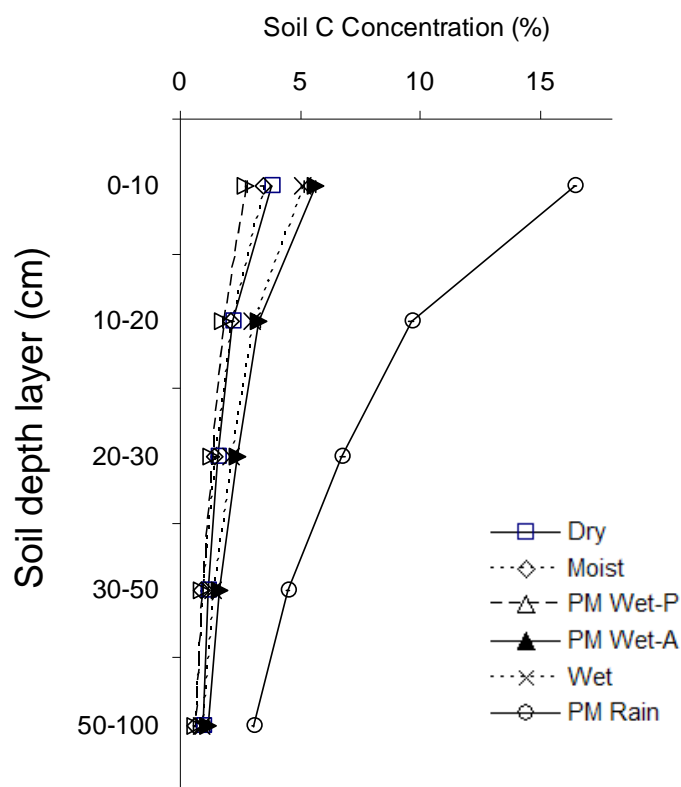


Figure 3.4. Mean soil carbon concentration (%) by depth layer interval (cm) in secondary forests growing in six life zones of Costa Rica. Life Zones are: Dry: Tropical Dry forest, Moist: Tropical Moist forest, PM Wet-P: Premontane Wet Transition to Basal forest - Pacific, PM Wet-A: Premontane Wet Transition to Basal forest - Atlantic, Wet: Tropical Wet forest, PM Rain: Premontane Rain forest.

Table 3.2. Ecosystem mass of carbon (Mg·ha⁻¹) in secondary forests growing in six life zones of Costa Rica.

Life Zone	Site Name	Age	Measured Carbon		Root C	TEC	Predicted Carbon		Mean Annual C Sequestration
			TAGC	Soil			Soil	Ecosystem	
Tropical Dry	Pitahaya	9	5.1	84.8 ± 12.1	1.5	91.4	45.8	52.4	5.8
	Bebedero	10	20.3	60.7 ± 11.5	4.6	85.6	47.7	72.6	7.3
	Pocosol	10	13.0	52.3 ± 5.8	3.7	68.9	47.7	64.3	6.4
	Mal Uso	14	23.5	138.6 ± 12.6	5.7	167.8	54.2	83.4	6.0
	Deep Throat	16	30.5	208.8 ± 14.7	7.3	246.6	57.1	94.9	5.9
	Firebreaks	17	9.5	77.8 ± 11.8	2.7	89.9	58.4	70.6	4.2
	Príncipe	22	40.5	101.8 ± 6.6	9.7	152.0	64.5	114.7	5.2
	Naranjo	26	58.1	188.8 ± 12.0	13.3	260.3	68.8	140.2	5.4
	Buen Uso	27	69.9	171.1 ± 7.4	15.8	256.8	69.8	155.5	5.8
	El Pozo	82	74.0	172.5 ± 22.9	18.5	264.9	106.9	199.4	2.4
	Primary Forest	--	73.0	124.2 ± 12.9	17.6	214.8	--	--	--
Tropical Moist	Downey	0.42	14.5	142.4 ± 13.1	2.5	159.4	22.0	39.1	n.c.
	Valle Azul	7	14.6	64.8 ± 3.6	3.4	82.9	44.5	62.6	8.9
	Caballos	7	32.4	174.3 ± 19.8	6.9	213.6	44.5	83.9	12.0
	Divino	9	32.4	95.8 ± 6.4	7.1	135.3	47.4	86.9	9.7
	Iguana	13	44.6	169.2 ± 11.3	9.8	223.6	52.0	106.5	8.2
	Quesera	16	54.3	113.4 ± 31.1	11.9	179.5	54.8	120.9	7.6
	Dubya	20	37.8	162.0 ± 11.4	8.9	208.7	57.9	104.6	5.2
	El Tanque	28	51.1	104.1 ± 18.7	11.9	167.1	63.0	126.0	4.5
	Santa Teresa	30	37.1	112.7 ± 7.6	9.0	158.8	64.1	110.2	3.7
	Chonco	40	41.9	132.4 ± 17.4	10.4	184.7	68.9	121.2	3.0
	Primary Forest	--	122.8	93.6 ± 14.0	28.7	245.1	--	--	--
Tropical	Yucal	2	9.7	191.4 ± 18.7	2.1	203.1	43.0	54.8	27.4
Premontane Wet,	Chupadero	6	14.6	107.7 ± 13.8	3.4	125.6	51.2	69.2	11.5
Transition to	Lapas	10	14.6	98.5 ± 6.9	3.5	116.7	55.6	73.8	7.4
Basal, Pacific	Hotel	15	50.6	88.7 ± 6.1	11.1	150.4	59.3	121.0	8.1
	Luciano	22	36.1	105.4 ± 11.0	8.6	150.1	63.1	107.9	4.9
	Primary Forest	--	122.8	93.6 ± 14.0	28.7	245.1	--	--	--

Table 3.2. (Continued)

Life Zone	Site Name	Age	Measured Carbon		Root C	TEC	Predicted Carbon		Mean Annual C Sequestration
			TAGC	Soil			Soil	Ecosystem	
Tropical	Cano	3	11.0	211.4 ± 17.7	2.5	224.9	45.9	59.3	19.8
Premontane Wet,	SAT 900	6	19.2	170.0 ± 5.3	4.4	193.6	51.2	74.9	12.5
Transition to	Con Permiso	10	42.7	216.2 ± 5.9	9.1	268.0	55.6	107.4	10.7
Basal, Atlantic	SAT 1000	15	41.8	167.2 ± 10.5	9.4	218.4	59.3	110.6	7.4
	Pao	21	67.0	184.7 ± 5.2	14.5	266.2	62.6	144.1	6.9
	Cascada	26	72.7	213.3 ± 8.5	16.0	302.0	64.8	153.5	5.9
	Sábalo	27	94.9	187.9 ± 14.3	20.3	303.1	65.2	180.4	6.7
	SHO 750	32	73.4	217.8 ± 10.1	16.5	307.8	67.0	156.9	4.9
	Primary Forest	--	137.9	193.9 ± 36.9	31.0	362.8	--	--	--
Tropical Wet	Terciopelo	0.7	8.0	197.2 ± 14.3	1.6	206.8	36.3	45.9	n.c.
	TUVA	1	8.1	118.4 ± 7.9	1.7	128.3	38.5	48.3	n.c.
	Culebra	3	19.5	180.5 ± 13.9	4.0	204.0	45.9	69.4	23.1
	La Huerta	6.5	40.2	124.6 ± 4.7	8.1	172.9	51.9	100.2	15.4
	Don Juan	9	39.9	208.8 ± 8.7	8.4	257.1	54.7	103.0	11.4
	Tirimbina	18	56.4	203.8 ± 9.5	12.2	272.4	61.1	129.7	7.2
	Piro	20	61.9	98.9 ± 4.6	13.4	174.1	62.1	137.4	6.9
	Pumilio	25	65.2	184.6 ± 4.9	14.3	264.1	64.4	143.9	5.8
	4 Ríos	29	118.1	170.1 ± 5.4	24.5	312.8	65.9	208.6	7.2
	Caliente	35	82.4	147.0 ± 11.3	18.2	247.5	68.0	168.5	4.8
	Palma Real	60	143.1	97.2 ± 10.2	31.3	271.6	74.1	248.5	4.1
	Primary Forest	--	215.0	125.0 ± 2.5	46.8	386.8	--	--	--

Table 3.2. (Continued)

Life Zone	Site Name	Age	Measured Carbon		Root C	TEC	Predicted Carbon		Mean Annual C Sequestration
			TAGC	Soil			Soil	Ecosystem	
Premontane Rain	Volcán	0.5	8.0	239.3 ± 12.2	1.5	248.8	34.4	43.9	n.c.
	Virgen María	10	37.0	278.3 ± 20.5	8.1	323.5	55.6	100.8	10.1
	Alemán	15	49.2	264.3 ± 11.2	10.9	324.4	59.3	119.4	8.0
	Cornelio	19	84.7	287.5 ± 20.4	18.0	390.2	61.6	164.3	8.6
	Milpa	20	68.2	258.0 ± 20.6	14.8	341.0	62.1	145.1	7.3
	Dos Ases	20	97.6	273.4 ± 4.5	20.5	391.5	62.1	180.2	9.0
	Cambronero	30	93.1	282.0 ± 10.1	20.5	395.6	66.3	179.9	6.0
	Hondura	35	88.6	315.3 ± 7.2	19.9	423.8	68.0	176.4	5.0
	Vargas	40	117.5	296.7 ± 16.3	25.9	440.2	69.4	212.9	5.3
	Kraven S.A.	50	108.3	289.7 ± 17.0	24.7	422.6	71.9	204.9	4.1
	Primary Forest	--	206.9	240.5 ± 52.5	46.3	493.7	--	--	--

Notes: TAGC ($\text{Mg}\cdot\text{ha}^{-1}$) represents total aboveground carbon. Soil C ($\text{Mg}\cdot\text{ha}^{-1}$) is the average soil C to 1 m depth (\pm SE). Soil C values were adjusted for compaction following Ayanaba *et al.* (1976) and Ellert & Bettany (1995) to allow direct comparisons with companion studies done in other land use categories in Costa Rica (Kauffman & Hughes, Jobse *et al.*, in prep.). Root C ($\text{Mg}\cdot\text{ha}^{-1}$) was calculated after Cairns *et al.* (1997) and assuming roots have 49% C content (Jackson *et al.* 1997). Total ecosystem carbon (TEC, $\text{Mg}\cdot\text{ha}^{-1}$) was calculated as the sum of measured TAGC, soil C, and root C. Predicted soil C to 25 cm depth ($\text{Mg}\cdot\text{ha}^{-1}$) was calculated using equations in Silver *et al.* (2000a). Predicted ecosystem carbon ($\text{Mg}\cdot\text{ha}^{-1}$) was calculated as the sum of TAGC, root C, and predicted soil C. Mean annual C sequestration rates ($\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) were calculated as the average of predicted ecosystem carbon and secondary forest age. n.c.: data not calculated.

Soil Carbon Pools

Measured soil C pools were 1.3 – 2.3 times larger in the Premontane Rain, Premontane Wet – Atlantic, and Wet life zones than in the three Drier life zones ($p < 0.0001$). There was considerable variation in the soil C pools to 1 m depth among sites within the life zones (Table 3.2). Soil C pools to 1 m depth ranged from 65 $\text{Mg}\cdot\text{ha}^{-1}$ in a 7 yr Moist forest to 315 $\text{Mg}\cdot\text{ha}^{-1}$ in a 35 yr Premontane Rain forest (Table 3.3). Secondary forests in the Dry, Moist and Premontane Wet - Pacific life zones had the lowest mean soil C pools to 1 m depth (118 to 127 $\text{Mg}\cdot\text{ha}^{-1}$). In contrast, mean soil C pools ranged from 157 $\text{Mg}\cdot\text{ha}^{-1}$ in Wet forests to 278 $\text{Mg}\cdot\text{ha}^{-1}$ in Premontane Rain forests (Table 3.3). We were unable to detect differences in soil C pools with forest age ($p = 0.8251$). Predicted soil C to 25 cm depth was 34 to 56 $\text{Mg}\cdot\text{ha}^{-1}$ in forests ≤ 10 yr, 64 to 66 $\text{Mg}\cdot\text{ha}^{-1}$ in forests 30 yr, and 74 $\text{Mg}\cdot\text{ha}^{-1}$ in a 60 yr Wet forest (Table 3.2).

The distribution of measured soil C was similar with depth across life zones. An average 31% of the soil C mass (52 – 100 $\text{Mg}\cdot\text{ha}^{-1}$) was concentrated in the top 0 – 10 cm soil depth layer of Dry forests (Table 3.3). In contrast, the proportion of total soil C in the 0 – 10 cm depth layer was $\sim 20\%$ in the remaining life zones (Table 3.3). Soil C to 10 cm depth ranged between 14 and 43 $\text{Mg}\cdot\text{ha}^{-1}$ in the Moist and Premontane Wet - Pacific life zones, and between 19 and 61 $\text{Mg}\cdot\text{ha}^{-1}$ in the Premontane Wet - Atlantic, Wet, and Premontane Rain life zones (Table 3.3). Across all life zones the top 0 – 20 cm soil depth layer contained an average ~ 30 to 60% of the total soil C pool to 1 m

depth. Soil C pools in the 0 – 20 cm depth layer represented 56% of the total soil pool to 1 m depth in Dry forests and 44% in Moist forests. In both Premontane Wet life zones and in the Tropical Wet life zone, soil C pools in the 0 – 20 cm depth layer represented 36 – 38% of soil C pools to 1 m depth (Table 3.3). In the Premontane Rain life zone, soil C in the 0 – 20 cm depth layer represented 31% of soil C pools to 1 m depth.

Although the average proportion of soil C pools to 20 cm depth among life zones ranged between 31 and 56% of soil C to 1 m, the absolute soil C pools were larger in Wetter life zones than in Drier ones. Average soil C pools to 20 cm depth ranged from 42 Mg·ha⁻¹ in Premontane Wet - Pacific forests to 55 – 61 Mg·ha⁻¹ in Moist and Dry forests and from 60 to 88 Mg·ha⁻¹ in the remaining life zones (Table 3.3). Soil C pools were highly correlated to mean annual temperature ($r^2 = -0.91$, $p < 0.0001$), elevation ($r^2 = 0.82$, $p < 0.0001$), and precipitation ($r^2 = 0.66$, $p < 0.0001$).

Carbon in Roots

In all life zones, the size of carbon pools in roots increased as forests aged (Table 3.2). Root C pools were generally smaller in secondary forests growing in Drier life zones than in Wetter ones. For example, Drier forests ~ 10 yr were predicted to have root C pools between 4 and 7 Mg·ha⁻¹ while root C pools in Wetter forests were 8 to 9 Mg·ha⁻¹ (Table 3.2). This difference became more pronounced with increasing forest age.

Forests 20 – 30 yr in the Drier life zones had root C pools of 9 to 16 Mg·ha⁻¹. In contrast, root C pools in forests 20 – 30 yr in the Wetter life zones ranged between 13 and 25 Mg·ha⁻¹ (Table 3.2). Despite these differences, root C pools were equivalent to 22 to 25% of TAGC pools in all life zones (Table 3.2). This proportion did not follow a trend with forest age (Table 3.2).

Total Ecosystem Carbon Pools

Measured total ecosystem C (TEC) pools ranged from 69 Mg·ha⁻¹ in a 10 yr Dry forest to 440 Mg·ha⁻¹ in a 40 yr Premontane Rain forest (Table 3.2). We found significant differences in TEC pools between life zones ($p < 0.0001$), with mean TEC ranging from 149 to 171 Mg·ha⁻¹ in Drier life zones, and between 228 to 370 Mg·ha⁻¹ in Wetter life zones. Because of the high variability in soil C pools (Table 3.3), we did not detect significant differences in measured TEC pools with secondary forest age in the Dry, Moist, Premontane Wet - Pacific, and Wet life zones ($p = 0.0768, 0.5144, 0.2044, 0.1620$, respectively). TEC sequestration in these life zones was largely a function of aboveground C gain (Table 3.2).

Table 3.3. Mass of soil carbon ($\text{Mg}\cdot\text{ha}^{-1}$) in secondary forests growing in six life zones of Costa Rica. Values are mean \pm SE.

Life Zone	Site Name	Age (yrs)	Depth interval (cm)					Total
			0-10	10-20	20-30	30-50	50-100	
Tropical Dry	Pitahaya	9	26.4 \pm 1.7	18.1 \pm 1.7	13.1 \pm 1.1	17.2 \pm 1.2	42.3 \pm 1.7	84.8 \pm 12.1
	Bebedero*	15	27.3 \pm 1.1	23.1 \pm 1.3	18.0 \pm 0.6	19.3 \pm 0.7	n.c.	60.7 \pm 11.5
	Pocosol*	15	28.7 \pm 1.9	25.4 \pm 1.7	16.1 \pm n.a.	n.c.	n.c.	52.3 \pm 5.8
	Mal Uso	14	36.7 \pm 1.7	30.9 \pm 1.7	23.0 \pm 0.7	35.1 \pm 0.7	64.7 \pm n.a.	138.6 \pm 12.6
	Deep Throat	16	41.2 \pm 3.2	33.5 \pm 1.4	25.6 \pm 1.6	38.0 \pm 3.8	70.3 \pm 6.9	208.8 \pm 14.7
	Firebreaks*	17	25.9 \pm 3.9	20.5 \pm 3.9	10.2 \pm 1.6	21.2 \pm 5.5	n.c.	77.8 \pm 11.8
	Príncipe*	22	37.1 \pm 4.5	28.0 \pm 3.5	21.3 \pm 4.1	25.7 \pm 3.7	n.c.	101.8 \pm 6.6
	Naranjo	26	45.7 \pm 7.3	29.8 \pm 5.9	23.0 \pm 2.1	37.5 \pm 2.6	52.9 \pm 2.3	188.8 \pm 12.0
	Buen Uso	27	36.0 \pm 2.5	29.6 \pm 1.4	22.1 \pm 1.0	31.1 \pm 1.4	52.1 \pm 4.3	171.1 \pm 7.4
Tropical Moist	El Pozo	82	34.3 \pm 3.9	32.0 \pm 4.1	28.0 \pm 3.0	45.4 \pm 6.0	54.6 \pm 2.3	172.5 \pm 22.9
	Downey	0.42	36.9 \pm 4.8	30.8 \pm 3.9	19.7 \pm 2.2	22.5 \pm 2.9	32.4 \pm 2.8	142.4 \pm 13.1
	Valle Azul	7	13.8 \pm 0.7	14.3 \pm 0.7	10.2 \pm 0.7	11.8 \pm 0.8	14.8 \pm 2.5	64.8 \pm 3.6
	Caballos	7	43.2 \pm 6.7	39.5 \pm 3.7	26.1 \pm 0.9	34.4 \pm 4.0	63.1 \pm 11.9	174.3 \pm 19.8
	Divino	9	20.1 \pm 0.4	20.4 \pm 0.8	16.0 \pm 1.6	18.8 \pm 2.8	20.4 \pm 2.3	95.8 \pm 6.4
	Iguana	13	35.8 \pm 1.9	32.4 \pm 1.8	22.9 \pm 2.4	27.3 \pm 2.0	50.8 \pm 7.0	169.2 \pm 11.3
	Quesera*	16	34.5 \pm 4.9	32.2 \pm 6.2	32.0 \pm 9.6	52.7 \pm 19.8	n.c.	113.4 \pm 31.1
	Dubya	20	33.8 \pm 2.8	31.1 \pm 2.4	23.2 \pm 2.2	29.7 \pm 2.5	44.2 \pm 3.9	162.0 \pm 11.4
	El Tanque	28	16.6 \pm 4.6	17.0 \pm 3.7	15.0 \pm 2.9	20.2 \pm 4.1	35.3 \pm 9.9	104.1 \pm 18.7
Premontane Wet Ttransition to Basal, Pacific	Santa Teresa	30	26.2 \pm 2.1	21.7 \pm 1.2	15.2 \pm 0.7	20.5 \pm 1.8	29.1 \pm 4.2	112.7 \pm 7.6
	Chonco	40	27.9 \pm 3.2	25.9 \pm 2.1	20.7 \pm 2.0	28.9 \pm 3.6	36.2 \pm 7.4	132.4 \pm 17.4
	Yucal	2	26.8 \pm 3.1	26.3 \pm 1.0	24.3 \pm 1.5	41.9 \pm 3.7	72.1 \pm 15.9	191.4 \pm 18.7
	Chupadero	6	21.6 \pm 1.8	21.2 \pm 2.1	16.4 \pm 1.8	23.8 \pm 3.7	30.9 \pm 6.6	107.7 \pm 13.8
	Lapas	10	19.9 \pm 1.0	19.9 \pm 1.2	14.4 \pm 1.2	19.9 \pm 2.2	24.4 \pm 3.5	98.5 \pm 6.9
Premontane Wet Ttransition to Basal, Atlantic	Hotel	15	13.6 \pm 2.1	14.1 \pm 1.6	12.8 \pm 1.0	14.3 \pm 1.1	33.9 \pm 5.7	88.7 \pm 6.1
	Luciano	22	24.9 \pm 2.7	20.6 \pm 1.7	15.1 \pm 1.4	18.1 \pm 2.4	26.6 \pm 4.6	105.4 \pm 11.0
	Cano	3	44.2 \pm 1.8	33.0 \pm 2.3	26.9 \pm 2.1	38.1 \pm 4.0	69.3 \pm 8.1	211.4 \pm 17.7
	SAT 900	6	37.7 \pm 4.3	29.1 \pm 2.3	23.5 \pm 1.6	31.7 \pm 1.9	48.0 \pm 3.7	170.0 \pm 5.3
	Con Permiso	10	54.7 \pm 3.1	38.6 \pm 3.5	27.2 \pm 1.7	33.8 \pm 1.2	62.0 \pm 2.3	216.2 \pm 5.9
	SAT 1000	15	34.4 \pm 5.8	26.3 \pm 1.9	20.7 \pm 0.4	29.8 \pm 1.0	55.9 \pm 3.4	167.2 \pm 10.5
	Pao	21	39.2 \pm 3.3	26.7 \pm 1.2	22.2 \pm 0.7	29.1 \pm 1.4	67.5 \pm 4.1	184.7 \pm 5.2
	Cascada	26	46.1 \pm 1.6	35.8 \pm 3.4	26.3 \pm 2.0	35.7 \pm 2.6	69.4 \pm 3.4	213.3 \pm 8.5
	Sábalo	27	39.7 \pm 2.7	27.1 \pm 2.0	22.3 \pm 1.3	32.9 \pm 2.8	65.9 \pm 5.9	187.9 \pm 14.3
Tropical Wet	SHO 750	32	53.0 \pm 3.9	33.2 \pm 1.5	26.3 \pm 1.5	36.6 \pm 3.2	68.7 \pm 4.4	217.8 \pm 10.1
	Terciopelo	0.7	32.9 \pm 2.2	33.4 \pm 1.7	25.8 \pm 1.7	37.2 \pm 3.8	68.0 \pm 6.9	197.2 \pm 14.3
	TUVA	1	19.1 \pm 0.8	22.3 \pm 1.0	15.1 \pm 0.9	28.0 \pm 2.3	34.0 \pm 4.3	118.4 \pm 7.9
	Culebra	3	33.1 \pm 3.0	32.5 \pm 2.8	24.5 \pm 2.2	32.3 \pm 1.8	58.0 \pm 5.4	180.5 \pm 13.9
	La Huerta	6.5	21.7 \pm 1.0	24.1 \pm 1.5	14.6 \pm 2.1	28.7 \pm 1.6	35.5 \pm 2.3	124.6 \pm 4.7
	Don Juan	9	39.1 \pm 2.9	36.1 \pm 2.6	29.2 \pm 2.4	38.5 \pm 1.9	65.9 \pm 2.4	208.8 \pm 8.7
	Tirimbina	18	41.2 \pm 2.1	35.6 \pm 2.4	26.5 \pm 1.8	39.9 \pm 1.5	60.6 \pm 3.2	203.8 \pm 9.5
	Piro	20	19.2 \pm 1.4	21.2 \pm 1.6	12.2 \pm 1.7	21.0 \pm 1.3	25.4 \pm 1.0	98.9 \pm 4.6
	Pumilio	25	40.6 \pm 1.7	32.9 \pm 1.6	24.3 \pm 0.9	31.0 \pm 1.3	55.7 \pm 3.1	184.6 \pm 4.9
	4 Ríos	29	31.7 \pm 1.8	29.4 \pm 0.7	23.2 \pm 0.8	31.7 \pm 2.2	54.1 \pm 2.8	170.1 \pm 5.4
	Caliente	35	32.2 \pm 2.6	36.0 \pm 2.4	22.1 \pm 4.0	29.4 \pm 2.1	27.2 \pm 3.6	147.0 \pm 11.3
	Palma Real	60	19.5 \pm 3.6	20.2 \pm 2.1	13.3 \pm 1.8	21.9 \pm 2.0	22.3 \pm 3.8	97.2 \pm 10.2

Table 3.3. (Continued)

Life Zone	Site Name	Age (yrs)	Depth interval (cm)					Total
			0-10	10-20	20-30	30-50	50-100	
Premontane Rain	Volcán	0.5	29.3 ± 2.3	31.4 ± 1.8	27.1 ± 3.2	57.3 ± 9.8	94.1 ± 6.6	239.3 ± 12.2
	Virgen María	10	43.2 ± 4.1	40.2 ± 2.1	37.3 ± 3.2	63.4 ± 3.7	94.2 ± 11.4	278.3 ± 20.5
	Alemán	15	52.0 ± 2.0	37.2 ± 1.2	31.6 ± 2.0	47.9 ± 2.1	95.7 ± 10.7	264.3 ± 11.2
	Cornelio	19	49.5 ± 3.3	32.9 ± 4.3	28.8 ± 2.0	61.8 ± 7.7	114.4 ± 10.8	287.5 ± 20.4
	Milpa	20	46.4 ± 3.0	38.7 ± 2.8	37.8 ± 3.3	60.3 ± 5.9	74.8 ± 11.5	258.0 ± 20.6
	Dos Ases	20	52.9 ± 3.4	39.8 ± 2.4	33.4 ± 1.5	48.4 ± 1.3	99.0 ± 7.4	273.4 ± 4.5
	Cambronero	30	51.3 ± 2.4	38.3 ± 2.5	31.5 ± 2.6	51.8 ± 3.0	109.2 ± 6.2	282.0 ± 10.1
	Hondura	35	47.3 ± 1.5	44.3 ± 1.6	42.6 ± 1.8	75.0 ± 2.5	106.1 ± 7.5	315.3 ± 7.2
	Vargas	40	60.7 ± 2.6	42.3 ± 4.0	39.6 ± 2.3	46.2 ± 3.1	107.8 ± 6.4	296.7 ± 16.3
	Kraven S.A.	50	54.4 ± 2.2	44.6 ± 2.3	41.5 ± 2.6	65.0 ± 4.3	84.2 ± 10.2	289.7 ± 17.0

Notes: "n.c" indicates samples were not collected; "n.a." indicates insufficient data to calculate SE. Total soil C in sites marked with "*" represents C pools to reported sampling depths.

The relative amount of measured TEC in secondary forests compared to that in primary forests varied across life zones. TEC in Dry forests ≥ 26 yr were $> 260 \text{ Mg}\cdot\text{ha}^{-1}$ (Table 3.2), or $\sim 20\%$ greater than those measured in primary forests (Kauffman and Hughes in prep.; Table 3.2). This may reflect site differences as primary forests are now largely restricted to marginal habitats which would result in lower C pools than what would occur if primary forests were growing on more productive sites currently used for agriculture. In contrast, TEC pools in forests > 26 yr in the Premontane Wet - Atlantic life zone were 83% ($302 \text{ Mg}\cdot\text{ha}^{-1}$, Table 3.2) of primary forest TEC pools. Similarly, TEC pools in 35 – 40 yr Premontane Rain forests represented close to 90% ($423 - 440 \text{ Mg}\cdot\text{ha}^{-1}$) of the TEC measured in primary forests (Table 3.2). Secondary forests in the Premontane Wet - Pacific life zone had the smallest TEC pools compared to those in primary forests, ranging from 116 to $150 \text{ Mg}\cdot\text{ha}^{-1}$, or about 50 to 60% of primary forest TEC in forests 10 and 22 yr,

respectively (Table 3.2). Overall, these results demonstrate secondary forests 20 – 30 yr-old growing in a diversity of climates sequester significant amounts of carbon.

Partitioning of Total Ecosystem Carbon

Soil is an important and large component of TEC. Measured soil C to 1 m depth comprised 71 to 79% of the TEC in all life zones. The average proportion of TEC in soils did not differ considerably between life zones, but it decreased as forests aged and aboveground C pools increased (Table 3.2). In the Moist life zone, for example, soils represented 89% of TEC ($159 \text{ Mg}\cdot\text{ha}^{-1}$) in a 0.42 yr forest and 72% of TEC ($185 \text{ Mg}\cdot\text{ha}^{-1}$) in a 40 yr forest (Table 3.2). Similarly, in the Premontane Wet - Atlantic life zone, soil C represented 94% of TEC ($225 \text{ Mg}\cdot\text{ha}^{-1}$) in a 3 yr forest and 71% ($309 \text{ Mg}\cdot\text{ha}^{-1}$) in a 32 yr forest (Table 3.2). In contrast, TAGC pools represented an increasing proportion of TEC with increasing secondary forest age. TAGC pools in forests ≤ 10 yr in all life zones represented an average 12% of TEC pools (range: 3 – 24%). In forests 20 – 30 yr, TAGC pools represented 22 to 38% of TEC pools.

Ecosystem Carbon Sequestration

Predicted ecosystem C was greater in Wetter life zones than in Drier ones. For example, predicted ecosystem C in forests ~ 10 yr in the Dry, Moist and Premontane Wet - Pacific life zones ranged between 52 and $87 \text{ Mg}\cdot\text{ha}^{-1}$. In contrast, in similarly-

aged forests, predicted ecosystem C was $101 - 107 \text{ Mg}\cdot\text{ha}^{-1}$ in the Wetter life zones (Table 3.2). This difference persisted as forests aged, with ecosystem C in Drier life zones reaching $110 - 156 \text{ Mg}\cdot\text{ha}^{-1}$, and Wetter life zones reaching $157 - 209 \text{ Mg}\cdot\text{ha}^{-1}$, in ~ 30 yr after pasture abandonment (Figure 3.2). Our estimates of predicted ecosystem C were smaller than TEC calculated based on field measurements (Table 3.2) because predicted ecosystem C only considered soil C pools to 25 cm depth. The differences were not related to forest age but were slightly larger in Wetter life zones and in Drier ones (Table 3.2). For example, mean predicted TEC was 40 to 46% of measured TEC in the Premontane Wet - Atlantic and Premontane Rain life zones. In contrast, mean predicted TEC was 67% of measured TEC in the Premontane Wet - Pacific and Dry life zones (Table 3.2).

Across life zones, mean annual rates of ecosystem C sequestration were significantly higher ($p < 0.0001$) in secondary forests ≤ 10 yr (mean = $11.5 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) than in older secondary forests. Mean annual C sequestration rates were $7.2 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in forests 20 yr and $5.7 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in forests 10 – 20 and 20 – 30 yr, respectively. Mean annual C sequestration rates were lowest in forests > 30 yr (mean = $3.9 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$; $p < 0.0109$, Figure 3.2).

Maximum rates of TEC sequestration were lowest ($7 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) in the Dry life zone and ranged from 14 to $33 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ as precipitation continued to increase. However, maximum rates of TEC sequestration declined to $12 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ at the wettest and

coolest extreme of our climatic gradient (*i.e.* the Premontane Rain life zone). We found a similar trend in mean sequestration rates of ecosystem C sequestration. Forests in the Dry, Moist, and Premontane Rain life zones had the lowest mean annual rates of C sequestration ($5 - 7 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) of all life zones. In contrast, mean annual sequestration rates ranged between 9 and $12 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ in the remaining life zones. Only mean annual C sequestration rates between the Dry and Wet life zones were statistically significant from each other ($p = 0.0030$).

Based on the ecosystem C of primary forests we expect highest C sequestration ($380 \text{ Mg}\cdot\text{ha}^{-1}$) in the Premontane Rain life zone (Figure 3.2). The Premontane Wet - Atlantic and Wet life zones will reach TEC between 268 and $331 \text{ Mg}\cdot\text{ha}^{-1}$, while the remaining life zones will reach TEC between 170 and $209 \text{ Mg}\cdot\text{ha}^{-1}$ (Figure 3.2, Kauffman & Hughes in prep.). We predicted secondary forests would attain ecosystem $C \geq 90\%$ of that in primary forests in 44 – 62 years in the Dry, Moist, and both Premontane Wet life zones (Table 3.4). In contrast, it would take 83 to 105 yr for secondary forests in the Premontane Wet – Atlantic and Premontane Rain life zone to reach TEC equivalent of that in primary forests (Table 3.4).

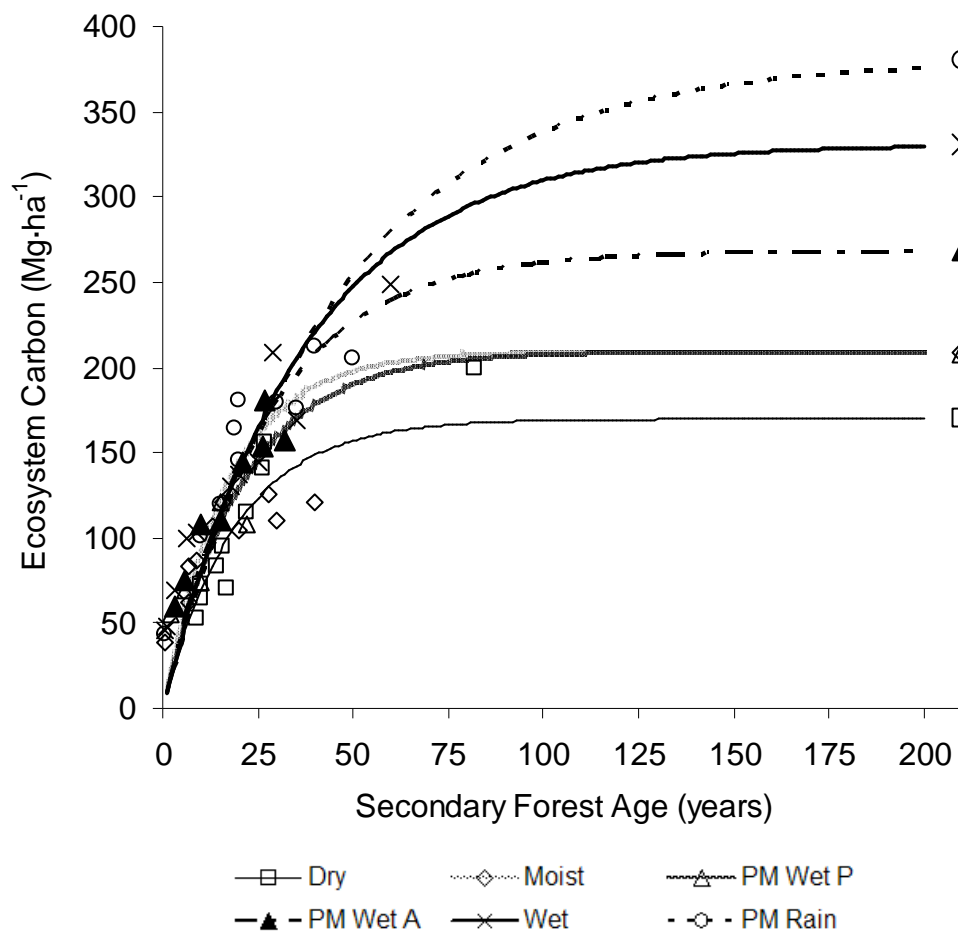


Figure 3.2. Ecosystem C (Mg·ha⁻¹) sequestration through time (years) in secondary forests of six life zones in Costa Rica. Curves represent natural growth functions fitted to the secondary forest ecosystem C data. Data points to the right represent ecosystem C in primary forests (Kauffman & Hughes in prep), including root C calculated after Cairns *et al.* (1997), and soil C to 30 cm depth (Kauffman & Hughes in prep.). Life zones are: Dry: Tropical Dry forest; Moist: Tropical Moist forest; PM Wet P: Premontane Wet Transition to Basal - Pacific forest; PM Wet A: Premontane Wet Transition to Basal - Atlantic forest; Wet: Tropical Wet forest; PM Rain: Premontane Rain forest.

Table 3.4. Equations for predicting ecosystem C ($\text{Mg}\cdot\text{ha}^{-1}$) sequestration in secondary forests growing in six life zones of Costa Rica.

Life Zone	EC_{max} ($\text{Mg}\cdot\text{ha}^{-1}$)	b_1 (yr^{-1})	n	Pseudo- R^2	Time to $\geq 90\%$ EC_{max} (years)
Tropical Dry	169.7	0.0520 (0.0055)	10	0.98	44
Tropical Moist	209.3	0.0381 (0.0058)	9	0.92	60
Tropical Premontane Wet, Transition to Basal - Pacific	209.3	0.0475 (0.0092)	5	0.93	48
Tropical Premontane Wet, Transition to Basal - Atlantic	268.2	0.0371 (0.0034)	8	0.98	62
Tropical Wet	330.7	0.0276 (0.0032)	9	0.95	83
Premontane Rain	380.2	0.0220 (0.0020)	9	0.97	105

Notes: Equations are of the form $\text{EC}_t = \text{EC}_{\text{max}} * [1 - \exp*(-b_1 * t)]$ (Sit & Poulin-Costello 1994). EC_t is the ecosystem C ($\text{Mg}\cdot\text{ha}^{-1}$) for secondary forests at time t (age of secondary forest, yr); EC_{max} is the ecosystem C ($\text{Mg}\cdot\text{ha}^{-1}$) measured in primary forests (Kauffman & Hughes in prep.), including root C calculated using equations from Cairns *et al.* (1997), and soil C to 30 cm depth (Kauffman & Hughes in prep.); b_1 is the rate at which ecosystem C approaches EC_{max} . Standard errors of regression coefficients (SE) are in parentheses. The equation for Tropical Premontane Wet Transition to Basal Pacific life zone was statistically significant at $\alpha = 0.0016$. Equations for all other life zones were statistically significant at $\alpha < 0.0001$. Pseudo- R^2 calculated after Schabenberger & Pierce (2001). Time to $\geq 90\% \text{EC}_{\text{max}} = -\ln(0.1)/b_1$ (Olson 1963).

Discussion

Tropical secondary forests play an important role in the sequestration of atmospheric C. However, explicit quantifications of total ecosystem carbon (TEC) pools in tropical secondary forests are extremely rare (Clark 2007). Studies of C dynamics have

concentrated on either above or belowground C pools. This is the first study to determine total ecosystem C pools and rates of sequestration of secondary forest stands growing along a broad gradient of tropical climates and to quantify the potential of these forests to sequester atmospheric carbon.

Total Aboveground Carbon

As predicted, we found smaller secondary forest TAGC pools and rates of sequestration in the Drier life zones than in Wetter ones. This is consistent with previous predictions of increasing C with greater water availability (Chapter 2, Silver *et al.* 2000a). TAGC in our study was smaller than the estimates given by Vargas *et al.* (2008) for Dry Mexican forests < 20 yr, but were larger in forests > 20 yr. Vargas *et al.* (2008) reported TAGC of 19 Mg·ha⁻¹ in a 9 yr forest and ~ 39 Mg·ha⁻¹ in forests ≥ 28 yr. In contrast, we measured TAGC of 5 and ≥ 70 Mg·ha⁻¹ in forests 9 and ≥ 27 yr, respectively (Table 3.2).

The TAGC measured in forests ≥ 26 yr in our study was similar to that measured in primary forests by Vargas *et al.* (2008) and those reported by Jaramillo *et al.* (2003). This is possibly a reflection of the smaller stature of the drier Mexican primary forests compared to forests at our Costa Rica sites, which are at the mesic extreme of Tropical Dry forest (Murphy and Lugo 1986). In contrast, TAGC we measured in Dry forests ≥ 26 yr was greater than in Costa Rican primary forests (Table 3.2, Kauffman &

Hughes in prep.). We suggest remaining Dry primary forests in Costa Rica have lower than expected TAGC because they are growing on marginal sites. In addition, the current fragmented nature of these forests (Arroyo-Mora *et al.* 2005) may have negatively affected their structure and reduced their aboveground biomass (Laurance 2004).

TAGC in Moist forests ranged from 15 Mg·ha⁻¹ in a 7 yr forest to 42 Mg·ha⁻¹ in a 40 yr forest (Table 3.2). These values represented < 23% of TEC and are lower than TAGC measured in other Moist forests. For example, TAGC in Brazilian forests ranged from 16 to 46 Mg·ha⁻¹ in 4 yr second- and third-growth forests (Hughes *et al.* 2000), 34 to 92 Mg·ha⁻¹ in forests 5 and 20 yr (Steininger 2000), 54 – 128 Mg·ha⁻¹ in forests 4 – 14 yr, and between 157 and 271 Mg·ha⁻¹ in 40 yr forests (Ferreira & Prance 1999). Our data is most comparable to that of regions where low soil nutrient concentrations, previous land-use history, or a combination of these factors negatively impact forest regrowth. Saldarriaga *et al.* (1988), for example, reported TAGC pools < 36 and 52 Mg·ha⁻¹ in forests < 20 and 30 – 40 yr growing in the oligotrophic Rio Negro Region of Colombia and Venezuela. For comparison, forests < 20 yr in our study averaged 33 Mg·ha⁻¹, and forests 30 – 40 yr ranged between 37 and 42 Mg·ha⁻¹. Similarly, Uhl *et al.* (1988) reported an average TAGC of 26 Mg·ha⁻¹ in 7 – 8 yr Brazilian forests growing in areas previously exposed to moderate pasture use intensity. We thus conclude Moist forests had sequestration rates at the low end of the

Neotropical Moist forests because of nutrient-poor soils, likely related to long legacies from previous land-use.

In the Wet life zone, TAGC pools were 8, 118, and 143 Mg·ha⁻¹ in forests ≤ 1, 29, and 60 yr, respectively (Table 3.2). These values are similar to Mexican Wet forests measured by Hughes *et al.* (1999), who found TAGC pools of 2, 122, and 136 Mg·ha⁻¹ in forests 0.5, 30, and 50 yr, respectively (Table 3.2). Our results are also comparable to those of Chacón *et al.* (2007), who measured 46 Mg·ha⁻¹ TAGC pools in a 15 yr Premontane Wet - Atlantic forest in Costa Rica.

This study is the first quantification of TAGC pools of tropical secondary forests growing in the Premontane Rain life zone. Thus, our estimates are not directly comparable with those reported for montane forests elsewhere in the tropics. Despite this limitation, our data are comparable to TAGC measured at other montane elevations. For example, we measured TAGC of 49 Mg·ha⁻¹ in a 15 yr Premontane Rain forest (Table 3.2), while Fehse *et al.* (2002) measured a TAGC of 45 Mg·ha⁻¹ in a 15 yr, *Polylepis*-dominated forest of Ecuador. In addition, we measured TAGC of 117 Mg·ha⁻¹ in a 40 yr Premontane forest, which is similar to the 116 Mg·ha⁻¹ measured by Fehse *et al.* (2002) in a 45 yr, *Alnus*-dominated forest of Ecuador. In contrast, Nadkarni *et al.* (2004) measured TAGC of 73 Mg·ha⁻¹ in a 40 yr Lower Montane Moist forest in Costa Rica. Additional TAGC data from Premontane and Montane

secondary forests are needed to further understand their potential to accumulate aboveground C.

Soil Carbon Pools

Mean soil C concentrations were higher in Wetter life zones (Table 3.3) than in Drier ones. Mean soil C concentrations to 1 m depth ranged from ~ 1% in Premontane Wet - Pacific and Moist forests to 6.6% in Premontane Rain forests (Appendix E). Primary forest soil C concentrations similarly ranged between 1.5 to 8.8% in Dry to Premontane Rain life zones respectively (Kauffman & Hughes in prep.). This increase in soil C along a climatic gradient of increasing precipitation and decreasing temperature is consistent with general patterns of global soil C described by Post *et al.* (1982) and Amundson (2001), and with gradients of soil organic matter in Costa Rican soils (Alvarado 2006).

Soil C pools were also higher in Wetter life zones than in Drier ones (Table 3.3). For example, mean soil C pools to 1 m depth ranged between 118 and 127 Mg·ha⁻¹ in the Premontane Wet - Pacific and Moist life zones, respectively. In contrast, mean soil C pools to 1 m depth ranged between 157 and 278 Mg·ha⁻¹ in Wet and Premontane Rain secondary forests, respectively (Table 3.3). Wetter life zones tend to have greater soil C pools than Drier ones because of higher rates of NPP (Silver *et al.* 2000a). Although direct comparisons are difficult to make because the diversity of methods used,

sampling of different depths (*e.g.* Johnson *et al.* 2001, Lugo *et al.* 1986), or even the use of horizons instead of fixed sampling depths (Guggenberger and Zech 1999, Vargas *et al.* 2008), our estimates are similar to soil C pools reported elsewhere in the tropics. Hughes *et al.* (1999), for example, measured soil C pools to 1 m depth of 139 – 269 Mg·ha⁻¹ in Wet secondary forests in Mexico, compared to our estimates of 99 to 209 Mg·ha⁻¹ for forests in the same life zone (Table 3.3). In addition, we measured an average soil C pool to 1 m depth of 119 Mg·ha⁻¹ in Moist forests, while de Camargo *et al.* (1999) reported 103 Mg·ha⁻¹ in a “closed capoeira” (secondary forest) in Brazil. In the Premontane Wet - Atlantic life zone of Costa Rica, Schedlbauer and Kavanagh (2008) reported soil C pools to 30 cm depth ranged between ~ 55 and 90 Mg·ha⁻¹. This was similar to the 97 Mg·ha⁻¹ reported by Daqui (2006, cited by Chacon 2008) and our own estimate of 98 Mg·ha⁻¹ for a similar soil depth (Table 3.3).

In contrast to conclusions from Brown & Lugo (1990) and Silver *et al.* (2000a), we could not find evidence that secondary forest soils accumulate or increase soil C after land use abandonment. The response of soil C pools to changes in tropical land cover from forest to agricultural lands of several types and back to forest is still equivocal and related to many site and land use factors (Guo & Gifford 2002, Murty *et al.* 2002). Some studies have documented increases of soil C pools after pasture abandonment (Bautista-Cruz & del Castillo 2005, Guggenberger & Zech 1999, Lugo *et al.* 1986, Silver *et al.* 2000a), while others have found the opposite trend (de Koning *et al.* (2003), for young secondary forests). Furthermore, de Camargo *et al.* (1999) found no

differences in soil C pools to 8 m depth between pastures, secondary forests, and a primary forest of Brazil. Similarly, Hughes *et al.* (1999) did not find changes in soil C pools along a sequence of land use types (*i.e.* pastures, pastures and cornfields, and secondary forests) in Mexico, and Schedlbauer & Kavanagh (2008) did not find increased soil C storage in a chronosequence of secondary forests 0 – 30 yr in Costa Rica. Most of the secondary forests we sampled were also < 30 yr (Table 3.2). Brown and Lugo (1990) and Conen *et al.* (2003) suggest > 40 yr may be required to detect changes in soil C. Chronosequence studies such as the ones we used may be too coarse to determine the rate of soil C accumulation if that rate is in the range of 0.2 – 1 Mg·ha⁻¹·yr⁻¹ reported by Silver *et al.* (2000a). This represents < 1% of the soil C pools we measured in Dry forests, a negligible amount of the soil C pools in the Premontane Rain life zone, and well within the errors of our sampling (Table 3.3).

Differences in soil type, texture, clay mineralogy, and OM complexes (Hughes *et al.* 1999, Powers & Schlesinger 2002, Silver *et al.* 2000b) within a life zone may have also impaired our ability to detect differences in soil C pools with secondary forest age. For example, Guggenberger and Zech (1999) documented soil C increased over succession in Inceptisols, while Hughes *et al.* (1999) found no changes in soil C while working in an area dominated by Andisols. Finally, differences in the type and intensity of land use can influence trends of soil C accumulation in secondary forests (Buschbacher *et al.* 1988, Fearnside and Barbosa 1988, Silver *et al.* 2000a), further

increasing the variability of soil C pools within a life zone and precluding us from detecting differences in soil C pools among forest ages.

Our results do not necessarily imply soils are in a static condition; changes in soil C fractions have been documented in soils following land use conversions (Ehleringer *et al.* 2000, Guggenberger & Zech 1999, Murty *et al.* 2002, Neill *et al.* 1997, Schedlbauer & Kavanagh 2008). For example, although de Camargo *et al.* (1999) found no differences in soil C pools to 8 m depth between pastures, secondary forests, and a primary forest of Brazil, the soil C fractions were different among these land cover types. We suggest isotopic measurements may provide a more sensitive indication of recovery of internal soil C cycling processes than do measures of soil C pools. In addition, we conclude our approach may not have been sufficient to control for variation in soil properties and detect subtle changes in soil C pools with increasing forest age (Post *et al.* 2001).

Total Ecosystem Carbon Pools

We found Wetter life zones had larger TEC pools than Drier ones (Table 3.2). TEC reported by Chacón *et al.* (2007) was 16% higher than our data for a 15 yr forest in the Premontane Wet - Atlantic life zone. Our TEC data for Wet forests (Table 3.2) were also lower than those reported by Hughes *et al.* (1999), who found TEC ranged from 156 to 348 Mg·ha⁻¹ in Wet forests 4 – 30 yr. In Mexican Dry forests, Vargas *et al.*

(2008) reported TEC, calculated with soil C pools to ~ 7 cm depth (Vargas, personal communication), ranged from 21 to 120 Mg·ha⁻¹ in 1 – 29 yr forests. In comparison, our TEC estimates, calculated with soil C pools to 10 cm depth, are similar, ranging between 31 to 112 Mg·ha⁻¹ for Dry secondary forests 9 to 27 yr (Table 3.3).

Measured soil C pools were large and varied considerably within life zones (Table 3.3), which impacted our ability to find differences in TEC with secondary forest age. For example, TEC pool in a 18 yr Wet forest was 10% greater than that measured in the older forest because of the large size of the soil C pool (Table 3.2). A similar situation was apparent in the Premontane Wet - Pacific life zone, where the large soil C pools in a 2 yr secondary forest resulted in it having greater TEC pools than older secondary forests (Table 3.2). Thus, we conclude that detecting changes in the size of TEC pools in secondary forests might only be possible when the variability in soil C pools along a chronosequence is low. This highlights the importance of controlling for soil variability, previous land-use history, and other intrinsic site factors to quantify the potential of secondary forests to regrow and accumulate C (Birdsey & Weaver 1987, Hughes *et al.* 1999, Uhl *et al.* 1988). In addition, it illustrates the difficulties of properly interpreting ecological patterns of recovery using chronosequences (Dewalt *et al.* 2000, Schedlbauer & Kavanagh 2008).

Predicting Ecosystem Carbon Sequestration

Our predictions of soil C to 25 cm depth are likely the largest source of bias in the calculation of predicted ecosystem carbon because soil C represents an average 44 to 67% of predicted TEC across all life zones (Table 3.2). Life zone-specific equations to predict soil C accumulation are available only for Dry and Moist climates, and we used a generic equation (Silver *et al.* 2000a) to predict soil C in the remaining life zones. However, soil C accumulation varies with environmental variables such as temperature (Raich *et al.* 2006) which suggests a single equation may be inadequate to predict soil C across a variety of climates. In addition, only the equation for Dry forests has high predictive power ($r^2 = 0.99$, compared to $r^2 = 0.11$ and 0.23 for the remaining equations; Silver *et al.* 2000a), adding to the uncertainty of estimating soil C.

Estimates of root C are also likely contributors to the uncertainty of potential TEC. In our study root C represented ~ 20% (range: 18 – 30%) of TAGC across all life zones (Table 3.2). However, roots represented 55% of TAGB secondary forests in the Premontane Moist life zone of Colombia (Sierra *et al.* 2007), between 6.8 and 8.5% of TAGB in Dry secondary forests in Mexico (Jaramillo *et al.* 2003), and between 13 and 21% of TAGB in Moist secondary forests of Colombia and Venezuela (Saldarriaga *et al.* 1988). The amount of root C apparently varies greatly across different sites, life zones, and possibly forest ages. Thus, a single equation for estimating root biomass,

such as the one proposed by Cairns *et al.* (1997), across a diversity of climates is inadequate for proper quantification of root C.

The C concentration in roots may also influence the size of our root C estimates. We calculated root C assuming their C content matches the global estimate of 49% C content (Jackson *et al.* (1997). However, published C concentrations of tropical roots vary from 39 to 50% C (Gifford 2000, Jackson *et al.* 1997, Jaramillo *et al.* 2003, Naddlehoffer & Raich 1992, Vargas *et al.* 2008). In addition, root C concentration was 38 and 42% C in roots ≤ 4 and 20 mm (Jaramillo *et al.* 2003), suggesting a single value for root C concentrations may not be adequate for properly calculating root C pools. Despite these sources of error, root C is likely a small contributor to the uncertainty around predicted TEC because it represents a mean of 4 – 5% (maximum 12% in a 60 yr Wet forest) of TEC across all life zones and forest ages. For example, assuming root C concentrations were 39% C, predicted TEC would decrease only by 1%. More attention needs to be devoted to quantifying belowground C in roots and mineral soil to improve our estimates of TEC accumulation in secondary forests.

We found ecosystem C sequestration rates were lowest at the dry and wet extremes of our climatic gradient. In our study, mean annual precipitation was ≤ 2500 mm in the Dry and Moist life zones, and reached 5200 mm in the Premontane Rain life zone (Castro 1992). While increased water availability promotes forest growth in Dry forests, increased mean annual precipitation in excess of 2445 mm may reduce forest

productivity by decreasing radiation inputs, increasing nutrient losses, or reducing soil oxygenation (Schuur 2003). Our mean and maximum sequestration rates suggest secondary forest growth responds positively to increased precipitation up to ~ 4100 mm and then declines, possibly because of interactions with higher mean annual temperature (Chapter 2, Brown & Lugo 1982, Raich *et al.* 2006).

Our data demonstrate how TAGC, and hence ecosystem C, increases with forest age. We also found that sequestration rates and C saturation levels differ among life zones. The potential of secondary forests to accumulate C may decrease in the future due to anticipated changes in climate for Costa Rica (Campos 1999, MINAE/IMN 1996). For example, reduced precipitation and higher temperatures may increase tree mortality (Clark 2004) and may even lead to widespread forest collapse due to drought and fire (Lewis 2006). In addition, greater air temperature could cause a decrease in soil C pools by accelerating decomposition rates (Raich *et al.* 2006), consequently offsetting the potential for secondary forest ecosystems to sequester atmospheric C. Long-term monitoring of ecosystem C pools (Clark 2007) in tropical forests would provide further insights into their ecophysiological response to global climate change. This would help resolve our understanding of whether potential C losses into the atmosphere from primary forest degradation, agriculture, and other human activities can be offset by secondary forest growth.

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CHAPTER 4

PREDICTING THE POTENTIAL OF TROPICAL SECONDARY FORESTS IN COSTA RICA TO MITIGATE CARBON LOSSES FROM PRIMARY FORESTS OVER A CENTURY OF CLIMATE CHANGE

Abstract

In addition to carbon losses into the atmosphere because of current deforestation and forest degradation, tropical primary forests may release more carbon because of future climate change. Secondary forests can accumulate large amounts of carbon and may thus be used to offset carbon losses from primary forest degradation. The amount of carbon released from primary forests typical of five life zones in Costa Rica under two possible climate scenarios until the year 2100 was calculated. Over the century, changes in the area of secondary forest and observed accumulation rates were used to calculate total aboveground carbon accumulation for each life zone. An expected 20% decrease in precipitation and a 4 °C increase in temperature across Costa Rica were predicted to result in a 65 Tg C loss from primary forests. Secondary forests would have to cover 19% of each life zone to offset this flux of C. Moist and Premontane Wet Transitional Forests would be expected to sequester the most carbon. Under similar warming conditions, but with precipitation decreasing by 20% in the Pacific region of Costa Rica while increased by 20% in the Caribbean region, the C loss from primary forests was predicted to be < 6 Tg. Already established secondary forests would sequester 23 Tg of C by 2100 under this climate scenario. The most likely climate scenario for Costa Rica is one of warming and drying conditions throughout the country. Consequently, reestablishment of secondary forests should be encouraged to minimize net carbon loss over the century.

Introduction

Deforestation constitutes a significant source of carbon from most tropical regions. Although the data vary depending on the methods used (Ramankutty *et al.* 2006), published estimates are as high as $2.2 \text{ Pg}\cdot\text{yr}^{-1}$ for the 1990s (Houghton 2003), which is similar in magnitude to the northern mid-latitude sink estimated by Gurney *et al.* (2002). In Costa Rica, strict laws instituted in the mid 1990s have resulted in the stabilization or increase of the total forest area (Calvo-Alvarado & Sánchez-Azofeifa 2007, Kleinn *et al.* 2002), which translates into limited or no carbon emissions from primary forest land use change.

Despite the stabilization of their area, primary forests can still be significant sources of carbon to the atmosphere because, in addition to the deleterious effects of fragmentation (Laurance 2004), ongoing climate change may further degrade primary forest structure and biomass (Clark 2004). If Costa Rica is to meet its goal to become carbon neutral by the year 2021 (Ruiz & Monge 2008), it must ensure that additional carbon emissions from degrading primary forests are balanced by sequestration efforts.

Secondary forests have the potential to sequester large amounts of carbon (Silver *et al.* 2002). In Costa Rica, a rapid decline in cattle ranching since 1990's (Arroyo-Mora *et*

al. 2005), coupled with government payments to encourage forest regeneration (Miranda *et al.* 2006), have led to an increase in secondary forests. These forests may now cover as much as 25% of the country (Kleinn *et al.* 2005) and have been estimated to sequester up to 300 – 400 Mg C·ha⁻¹ in 30 years after pasture abandonment (Chapter 3).

Estimates of carbon sequestration by secondary forests are generally made with the assumption that the total aboveground carbon (TAGC) historically reported for primary forests (C_{\max}) is a reasonable and attainable restoration goal (Chapter 3, Hughes *et al.* 1999, Vargas *et al.* 2008). C_{\max} represents the potential of TAGC for a specified type of tropical forest under this assumption. However climate change is likely to affect the dynamics of current and future forests (Clark 2004, Lewis 2006, Wright 2005). It is thus necessary to determine whether secondary forests growing in a variety of tropical climates will maintain their potential to act as carbon sinks and offset carbon losses from primary forest degradation due to climate change.

In this study we propose: (1) to calculate the amount of C that would be released into the atmosphere from primary forests in the next century under predicted changes in climate, and (2) to estimate whether secondary forests would be able to sequester enough atmospheric C to offset the loss from primary forests. We used a relationship established between annual mean temperature and precipitation with total aboveground carbon to predict gradual changes in C_{\max} to the end of this century. In

addition, we analyzed C_{\max} on a yearly time-step to calculate the net C accumulated by secondary forests. Our simulation does not consider changes in the frequency or intensity of disturbance events (*e.g.* ENSO, fires, etc.), which would further affect the C balance.

Methods

Climate and Total Aboveground Carbon in Primary Forests

We used the NLIN procedure in SAS 9.1.3 (SAS Institute 2000) to describe the relationship between primary forest total aboveground carbon (C_{\max} , $\text{Mg}\cdot\text{ha}^{-1}$, Kauffman & Hughes in prep.) and the ratio of mean annual temperature (T , $^{\circ}\text{C}$) to mean annual precipitation (P , mm) for primary forests of Costa Rica. Mean annual T and P for each life zone were derived from Castro (1992). This ratio (T/P ratio) serves as a simple index of potential availability of water to plants in an ecosystem. A more precise index of water availability to plants is the ratio of potential evapotranspiration to precipitation (Brown & Lugo 1982), but the data needed to calculate this ratio were lacking. Tropical Dry forests in Costa Rica grow under more mesic conditions than other Dry forests in tropical America (Murphy & Lugo 1986). Thus, to extend the T/P ratio vs. C_{\max} relationship to drier forests elsewhere in the tropics, we used data from Jaramillo *et al.* (2003), and Delaney *et al.* (1997).

Current and Future Total Aboveground Carbon

Calculations of total C pools for a life zone, C_{\max} and secondary forest TAGC were restricted to the Tropical Dry, Tropical Moist, Premontane Wet Transition to Basal, Tropical Wet, and Premontane Rain forest life zones (Holdridge 1967) of Costa Rica. Together, these life zones represent a climatic gradient ranging from hot and dry to cool and wet conditions. The current area of primary and secondary forest for each life zone was obtained by overlaying the most recent forest cover (Calvo-Alvarado & Sánchez Azofeifa 2007) and the Holdridge Life Zone (Bolaños & Watson 1993) maps for Costa Rica in a GIS (Vicente Watson, unpublished data). We calculated C pools for each life zone by multiplying the TAGC of primary (Kauffman & Hughes, in prep.) and secondary forests (Chapter 3) by their corresponding area (Table 4.1). Calvo-Alvarado and Sánchez-Azofeifa (2007) classified secondary forest ages as < 5, < 15 yr, and “secondary growth”. Given historical patterns of land use and abandonment in Costa Rica (Berti 2001), we assumed forests in the “secondary growth” category were all 30 years old. We also assumed the proportion of secondary forests of different ages reported by Calvo-Alvarado and Sánchez Azofeifa (2007) was constant for all life zones because data describing the age distribution of secondary forests within most life zones are lacking. TAGC of secondary forests was then calculated by partitioning the area within a life zone by age categories and multiplying the resulting areas by their corresponding C pools. Current secondary forest TAGC for

each age category was calculated by fitting the Chapman-Richards function (Richards 1959, Sit & Poulin-Costello 1994) to data from Chapter 3 of this dissertation (Table 4.2).

Table 4.1. Area (x 1000 ha) of five life zones and two forest types of Costa Rica under current and predicted climate by the year 2100.

Life Zone	Current Climate			Predicted Climate Scenarios by 2100			
	Total Life Zone	Primary Forest	Secondary Forest	Life Zone Scenario 1	% Change	Life Zone Scenario 2	% Change
Tropical Dry	116	41	5	724	623	674	580
Tropical Moist	715	214	47	2381	333	858	120
Premontane Wet							
Transition to Basal	707	190	18	940	133	530	-25
Tropical Wet	833	452	18	233	-72	1583	190
Premontane Rain	437	319	5	0	-100	568	130

Notes: Current area of life zones by Bolaños and Watson (1993) and current area of primary and secondary forest by Vicente Watson (unpublished data) derived from GIS data. Scenario 1: Area of life zone calculated assuming a 20% decrease in precipitation (P) and an increase of 4 °C in temperature throughout Costa Rica. Scenario 2: Area of life zone calculated assuming a 20% decrease in P in the Pacific region of Costa Rica, a 20% increase in P in the Atlantic region of Costa Rica, and an increase of 4 °C in temperature throughout Costa Rica. Climate Scenarios 1 and 2 correspond to “Dry 20/4” and “Dry-Wet 20/4” scenarios, respectively, by Enquist (2002).

To predict future TAGC pools, we used two climate scenarios developed by Enquist (2002) for Costa Rica. Under Scenario 1, a 20% decrease in precipitation and an increase in temperature of 4 °C is expected throughout the country. Scenario 2 predicts a 20% decrease in precipitation in the dry Pacific region of Costa Rica, with a concurrent 20% increase in precipitation for the wet Caribbean region, and a 4 °C increase in temperature across the entire country by the year 2100. Current temperature and precipitation were modified to match these climate scenarios, and the

T/P ratio for each life zone was recalculated accordingly. To match these projected future climatic conditions by the year 2100, we assumed precipitation and temperature would change at a constant rate of ± 42 mm and $+ 0.43$ °C per decade, respectively. No other disturbances that could alter forest growth dynamics were considered.

Table 4.2. Equations for predicting total aboveground carbon (TAGC, $\text{Mg}\cdot\text{ha}^{-1}$) in secondary forests growing in five life zones of Costa Rica.

Life Zone	C_{\max} ($\text{Mg}\cdot\text{ha}^{-1}$)	b_1 (yr^{-1})	b_2	n	Pseudo- R^2
Tropical Dry	73.0	0.1128 (0.0330)	5.4029 (3.2912)	10	0.95
Tropical Moist	122.8	0.0343 (0.0390)	1 --	10	0.95
Tropical Premontane Wet, Transition to Basal	137.9	0.0304 (0.0024)	1 --	8	0.98
Tropical Wet	215.0	0.0183 (0.0015)	1 --	11	0.97
Premontane Rain	206.9	0.0199 (0.0016)	1 --	10	0.97

Notes: Equations are of the form $\text{TAGC}_t = C_{\max} * [1 - \exp(-b_1 * t)]^{b_2}$ (Sit & Poulin-Costello 1994). TAGC_t is the TAGC ($\text{Mg}\cdot\text{ha}^{-1}$) for secondary forest at time t (age of secondary forest, yr), C_{\max} is the TAGC measured in primary forests of a given life zone, b_1 is the rate at which TAGC approaches C_{\max} , b_2 is the inflexion parameter of the curve. The equation with b_1 and b_2 parameters is a Chapman-Richards function fit, whereas equations with only parameter b_1 are natural growth function fits. Standard errors of regression coefficients (SE) are in parentheses. Equations were statistically significant at $\alpha < 0.0001$. Pseudo- R^2 calculated after Schabenberger & Pierce (2001).

We then calculated the TAGC of primary forests within a life zone under the two climate scenarios using the T/P ratio to C_{\max} regression (Figure 4.1), assuming the area of primary forest will remain constant into the year 2100. We compared current and

future TAGC of primary forests for each life zone to determine the loss of C. We used non-linear functions (Table 4.2) to predict secondary forest TAGC in each life zone. To accommodate the assumption of continuous climate change into the year 2100, C_{\max} in the Chapman-Richards function (Table 4.2) was adjusted to the T/P ratio calculated on a yearly time step. Finally, we assumed the area of secondary forests would increase over time at a constant annual rate. We manipulated this rate such that 5, 10, 15, 20, or 25% of the area of a life zone would be occupied by secondary forests in 2100. This increase in forest area is consistent with Costa Rica's current policy of promoting forest regeneration (Pagiola 2008, Zbinden & Lee 2005). We assumed secondary forests would not exceed 25% of the area of a life zone based on data from field inventories (Kleinn *et al.* 2005). We then used a time matrix of increasing secondary forest area and decreasing C_{\max} to calculate secondary forest TAGC for each life zone by the year 2100. To serve as a reference, we also calculated secondary forests TAGC assuming climate would remain unchanged to 2100.

Results

Climate and Total Aboveground Carbon in Primary Forests

We found a strong relationship between TAGC of primary forests and the T/P ratio (Figure 4.1; pseudo- $R^2 = 0.97$, $p < 0.0001$). Primary forests growing in life zones with

higher precipitation (*i.e.* Tropical Wet and Premontane Rain forests) had greater TAGC than Moist and Dry forests (Figure 4.1).

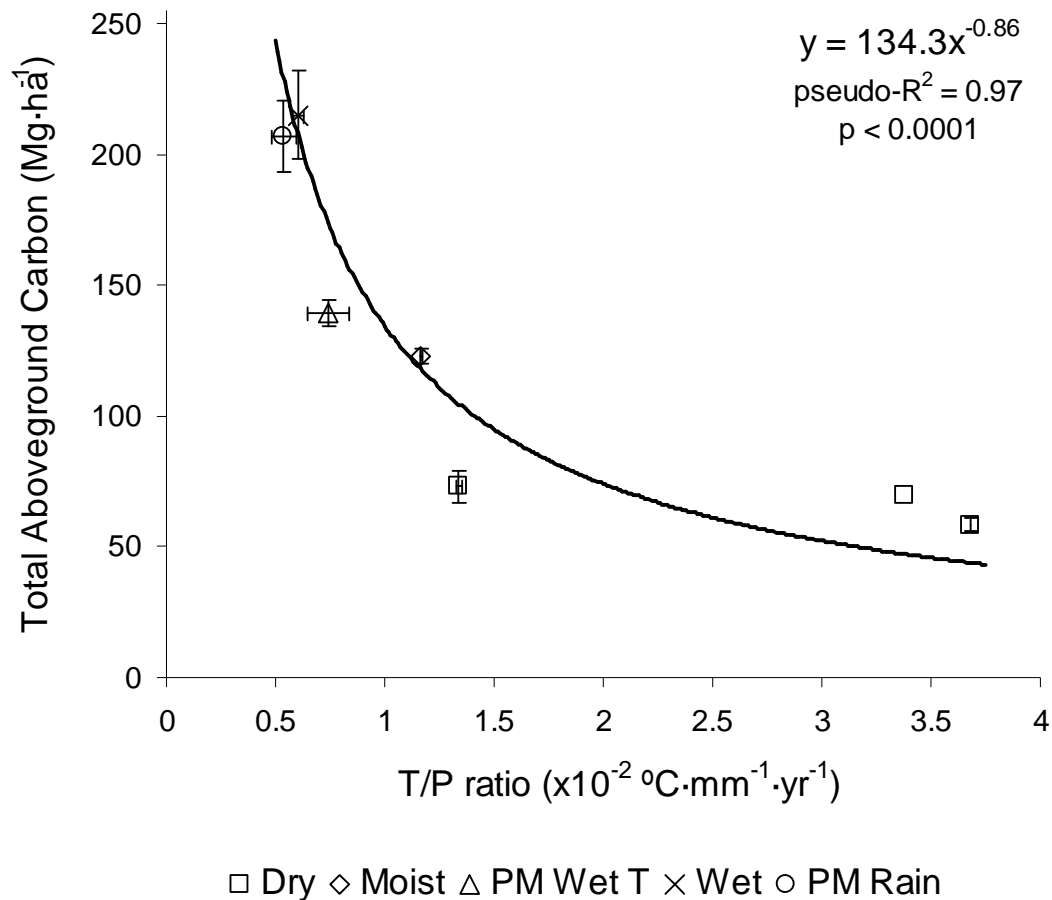


Figure 4.1. Relationship between total aboveground carbon (TAGC, Mg·ha⁻¹) of primary forests and the mean annual temperature (T, °C) to mean annual precipitation (P, mm) ratio (T/P ratio). The two data points to the far right are from Jaramillo *et al.* (2003) and Delaney *et al.* (1997); remaining data from Kauffman & Hughes (in prep.). Error bars represent ± 1 SE. Pseudo-R² = 1 - (SSE/SST) (Schabenberger & Pierce 2001). Life zones are: Dry: Tropical Dry forest, Moist: Tropical Moist forest, PM Wet T: Premontane Wet Transition to Basal forest, Wet: Tropical Wet forest; PM Rain: Premontane Rain forest.

Total Aboveground Carbon in Primary Forests

Under current conditions, TAGC of primary forests within a life zone was smallest in the Dry life zone (4 Tg), intermediate in the Moist and Premontane Wet Transition to Basal life zones (25 and 33 Tg, respectively), and largest in the Wet and Premontane Rain life zones (73 and 94 Tg, respectively, Figure 4.2).

In general, the aboveground C pools of primary forests in Costa Rica are expected to decline over the coming century. Under Scenario 1 and across all life zones, TAGC of all primary forests decreased to 71 to 73% of their original values. The largest decrease in TAGC is projected to occur primarily in the Wet (26 Tg) and secondarily in the Premontane Rain life zone (21 Tg, Figure 4.2). In contrast, TAGC should decrease by only 1 Tg in the Dry primary forests, and by 9 and 7 Tg in the Premontane Wet Transition to Basal and Moist primary forests, respectively. Overall, primary forest C pools in the five life zones would decrease by 65 Tg (Figure 4.2).

Under both climate scenarios, TAGC of primary forests in the Dry and Moist life zones would be 3 and 18 Tg, respectively (Figure 4.2). These pools would be the same regardless of the scenario because both assume similar changes in precipitation and temperature for the two life zones. Under Scenario 2, TAGC in Premontane Wet Transition to Basal, Wet, and Premontane Rain forests should remain constant or

increase slightly compared to current climate (~ 1 Tg, Figure 4.2). Under Scenario 2, the net C loss from primary forests for the five life zones would be < 6 Tg (Figure 4.2).

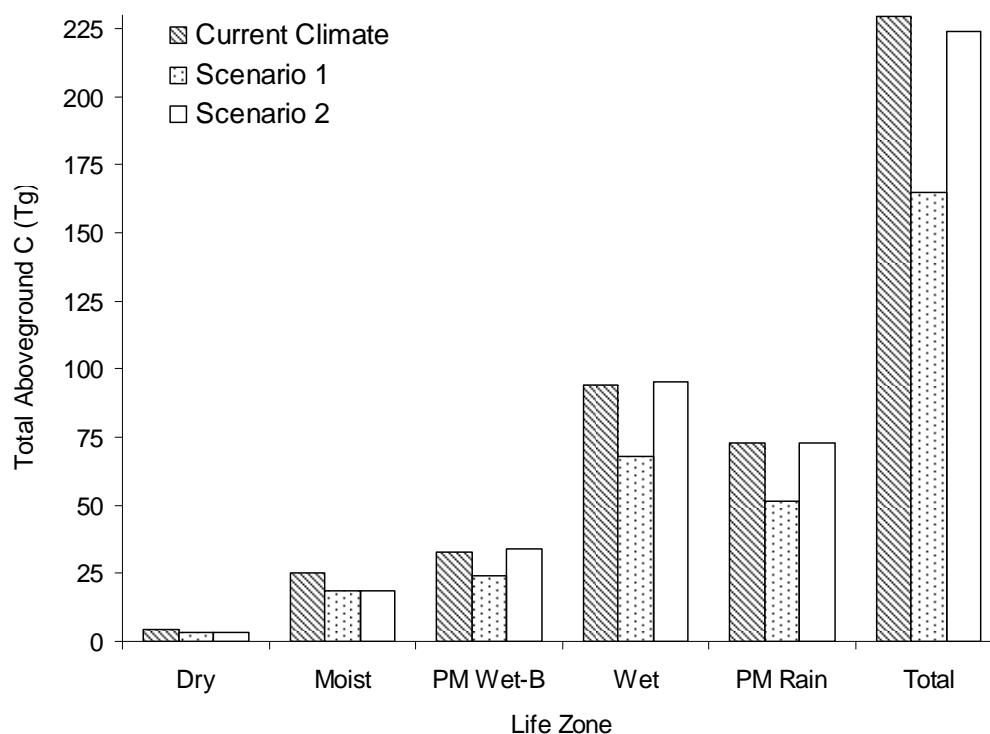


Figure 4.2. Total aboveground carbon (TAGC, Tg) in primary forests growing in 5 life zones of Costa Rica under current climate conditions and two potential future climate scenarios. Current Climate represents existing TAGC; Scenario 1 represents TAGC calculated assuming a 20% decrease in precipitation (P) and an increase of 4 °C in temperature throughout Costa Rica; Scenario 2 represents TAGC calculated assuming a 20% decrease in precipitation (P) in the Pacific region of Costa Rica, a 20% increase in P in the Atlantic region of Costa Rica, and an increase of 4 °C in temperature throughout Costa Rica. Climate scenarios 1 and 2, and future area of each life zone correspond to “Dry 20/4” and “Dry-Wet 20/4” scenarios, respectively, by Enquist (2002). Life zones are: Dry: Tropical Dry forest; Moist: Tropical Moist forest; PM Wet-B: Premontane Wet Transition to Basal forest; Wet: Tropical Wet forest; PM Rain: Premontane Rain forest. Total bars represent the sum of TAGC across the 5 life zones.

A reduction in precipitation coupled with warmer temperatures would have a disproportionate negative effect on the total aboveground C of primary forests compared with increasing both temperature and precipitation. For example, in Scenario 1, primary forest TAGC pools in the Premontane Rain and Wet life zones declined by 21 and 26 Tg (Figure 4.2). In contrast, in Scenario 2, primary forest TAGC was predicted to remain unchanged in the Premontane Rain life zone and to increase by only 1 Tg in the Wet life zone.

Total Aboveground Carbon in Secondary Forests

If we assume the area of secondary forest within a life zone remains constant, the Moist life zone had the most gain in TAGC across all climate scenarios (Table 4.3). However, TAGC for the Moist life zone under Scenarios 1 and 2 was 72% of that calculated under current conditions. We found a similar reduction in TAGC in the Dry and Premontane Wet Transition to Basal life zones. For example, in the Premontane Wet Transition to Basal life zone, TAGC decreased from 6 Tg under current conditions to 4 Tg under Scenario 1 (Table 4.3). In contrast, TAGC in the Premontane Wet Transition to Basal life zone was 5% larger under Scenario 2 than under current conditions. Secondary forest TAGC in the Wet life zone under Scenario 1 was 71% of that under current conditions (Table 4.3). In comparison, TAGC was only 1% greater in the Wet and Premontane Rain life zones under Scenario 2 than under current

conditions. When comparing across all five life zones, secondary forest TAGC calculated under current conditions was 1.1 and 1.5 more than under Scenarios 2 and 1, respectively (Table 4.3). In other words, relative to current conditions, we would expect an overall reduction of secondary forest TAGC pools in response to projected changes in climate.

Across all climate scenarios and life zones, TAGC increased as the area of secondary forests increased. Under Scenario 1, TAGC pools of secondary forests in the Premontane Wet Transition to Basal and Moist life zones was predicted to be the largest among all life zones when secondary forests were assumed to cover 25% of each life zone, reaching 24 and 40 Tg, respectively (Table 4.3). Under Scenario 1, TAGC in the Moist and Dry life zones would be expected to be 1.5 and 4 times larger than under current climatic conditions (Table 4.3) because the area of these life zones are predicted to increase significantly (Table 4.1). In contrast, under Scenario 1, the Wet life zone would have the lowest TAGC of all life zones, ranging from 4 to 8 Tg as secondary forest cover increases from 5 to 25% of the life zone (Table 4.3).

Table 4.3 Total aboveground carbon (TAGC, Tg) of secondary forests by the year 2100 in five life zones of Costa Rica under current climate conditions and two climate scenarios. TAGC calculated using current area of a life zone under secondary forest cover and as a function of the total area of a life zone (%) covered by secondary forests in 2100.

		Percent of the life zone covered by secondary forests by the year 2100				
Life Zone	Current Area	5	10	15	20	25
<i>Current Climate Conditions</i>						
Tropical Dry	1.1	1.1	1.6	2.0	2.5	3.0
Tropical Moist	10.5	9.7	12.6	15.5	18.4	21.3
Premontane Wet Transition to Basal	5.8	7.9	12.0	16.0	20.0	24.1
Tropical Wet	6.2	11.8	16.4	21.0	25.6	30.2
Premontane Rain	2.1	4.1	6.8	9.5	12.2	14.9
Total	25.7	34.7	49.4	64.0	78.7	93.5
<i>Climate Scenario 1</i>						
Tropical Dry	0.8	2.7	4.9	7.1	9.3	11.5
Tropical Moist	7.6	6.9	18.9	25.8	32.9	39.9
Premontane Wet Transition to Basal	4.3	7.0	11.1	15.3	19.5	23.7
Tropical Wet	4.4	4.4	4.9	5.8	6.8	7.7
Premontane Rain	0.0	0.0	0.0	0.0	0.0	0.0
Total	17.1	21.0	39.7	54.1	68.4	82.7
<i>Climate Scenario 2</i>						
Tropical Dry	0.8	2.5	4.6	6.6	8.7	10.7
Tropical Moist	7.6	6.9	9.9	12.4	14.9	17.5
Premontane Wet Transition to Basal	6.1	7.3	10.6	13.9	17.3	20.6
Tropical Wet	6.3	13.2	22.2	31.1	40.1	49.1
Premontane Rain	2.1	5.2	8.8	12.5	16.2	20.0
Total	22.8	35.1	56.0	76.6	97.2	117.8

Notes: Current area: TAGC projected by the year 2100 assuming no increase in secondary forest area from current area. Current Climate Conditions: TAGC calculated assuming current climate persists into the year 2100 but area of secondary forests increases. Climate Scenario 1: TAGC calculated assuming a 20% decrease in precipitation (P) and an increase of 4 °C in temperature throughout Costa Rica. Climate Scenario 2: TAGC calculated assuming a 20% decrease in precipitation (P) in the Pacific region of Costa Rica, a 20% increase in P in the Atlantic region of Costa Rica, and an increase of 4 °C in temperature throughout Costa Rica. Climate scenarios 1 and 2 correspond to “Dry 20/4” and “Dry-Wet 20/4” scenarios, respectively, by Enquist (2002). TAGC in the Premontane Rain life zone under Scenario 1 is zero because the life zone is expected to disappear (Enquist 2002).

By increasing the area of secondary forests, some of the C lost from primary forests could be offset. Under Scenario 1, we calculate that secondary forests would need to cover ~ 19% of each life zone by 2100 to offset the loss of C resulting from the decline in the amount of primary forest biomass associated with climate change (65 Tg, Figure 4.2). Under such conditions, secondary forests in the Moist and Premontane Wet Transition to Basal life zones are predicted to sequester 32 and 19 Tg C whereas Dry secondary forests would sequester 9 Tg and Wet secondary forests, 7 Tg. Under Scenario 2, growth of currently established secondary forests alone would sequester 23 Tg of C by 2100 (Table 4.3). If the area of secondary forests increased to 25% of each life zone, then secondary forests growing under Scenario 2 in the five life zones of this study, could accumulate 118 Tg of C by 2100 (Table 4.3). This implies that, depending on future climate conditions, secondary forests would not only offset C losses from primary forests but could act as a large net C sink.

Discussion

Uncertainties in Calculating Total Aboveground Carbon in Costa Rican Forests

The magnitude, direction, and timing of primary forest responses to climate change are subject to much debate. Phillips *et al.* (2004) reported increasing atmospheric CO₂ concentrations have, in recent decades, accelerated forest dynamics and increased live

aboveground biomass in the Brazilian Amazon. This increase in TAGC will likely decline, however, as forest growth becomes limited by other resources such as soil nutrients and water (Lewis 2006). In addition, increasing respiration costs due to higher temperatures could cause tropical forests to ultimately become a source of carbon to the atmosphere (Lewis 2006). We assumed that primary forests are already responding negatively to warmer and drier climate (Clark 2004). If this is not the case, we may be overestimating the loss of C from primary forests into the atmosphere.

A limitation of our simulations is that they do not consider that disturbance and its effects may change over time. For example, if climatic disturbances associated with strong ENSO events caused increased tree mortality via enhanced drought, a net loss of carbon would result (Rolim *et al.* 2005, Williamson *et al.* 2000). Also, drier and warmer climate, combined with forest fragmentation, increases the risk of fire and would significantly reduce forest C pools (Guariguata *et al.* 2008, Laurance 2004). Furthermore, fire can significantly change the successional pathways of secondary forests (Mesquita *et al.* 2001). Rising CO₂ in the atmosphere appears to favor growth of lianas, which could further impede forest recovery, raise tree mortality rates, and lower forest biomass (Gerwing 2002, Lewis *et al.* 2004). Finally, if annual rainfall were to fall below a critical threshold of < 1500 – 2000 mm (Lewis 2006), tropical forests might be replaced by savannas (Mayle *et al.* 2004, Salzmänn & Hoelzmann 2005). All these mechanisms would lower C_{max} beyond the predicted impacts of climate change alone, and we would be underestimating the amount of C released into

the atmosphere through forest degradation. Because disturbance can also negatively affect succession, we would also be underestimating the amount of C potentially fixed by secondary forests.

Estimates of the area of Costa Rica currently covered by secondary forests as well as the age distribution of these forests are uncertain. For example, using forest cover maps by Calvo-Alvarado & Sánchez Azofeifa (2007), secondary forests cover 3.3% of the country. In contrast, Kleinn *et al.* (2005), who used field inventories, reported 25% of the land area Costa Rica is covered by secondary forests. The former dataset may be an underestimate because passive remote sensing cannot distinguish between secondary forests > 15 yr and primary forests (Lu 2006). This implies the current area of primary forest, and thus their current and future C pools within a life zone may be significantly overestimated in our analysis.

The difficulties involved in using remote sensing to determine the age of secondary forests > 15 yr after agricultural abandonment likely explain some of the discrepancy in predicted areas of secondary forests and thus our TAGC estimates for each life zone. However, the influence of forest age on landscape-scale estimates of C is likely to be small because older secondary forests have lower rates of carbon increment than younger ones (Chapter 3). For example, the difference in estimates of TAGC for secondary forests with current ages of 30 or 50 years, when extended to 2100, differ by only 1 – 5%. Errors in estimation of area supporting secondary forests will affect

TAGC predictions much more. We demonstrated this by showing that, under constant climatic conditions, secondary forest TAGC pools by 2100 were 1.3 times larger than our first estimates (Current Area, Table 4.1) when we tripled the current area of secondary forests > 15 yr. To improve our C sequestration estimates, we emphasize the need to quantify the age structure of secondary forests more accurately.

Potential of Secondary Forests to Sequester Carbon

When we assumed current secondary forest area would remain constant to 2100 we found a shift in climate to less precipitation and warmer temperature (*i.e.* Scenario 1 and Dry and Moist life zones in Scenario 2) had a large negative effect on TAGC. This conclusion is supported by the work of Nepstad *et al.* (2002) who documented a 25% decrease in NPP in a drought experiment in Brazil. In addition, Williamson *et al.* (2000) reported a 70% increase in tree mortality rates in the Amazon following a severe El Niño drought. Clark (2004) suggested the combined responses of photosynthesis and respiration to increasing temperature could result in strong reductions in NPP and a shift in NEE towards C emissions. In contrast, our simulations indicate that by increasing both temperature and precipitation (*i.e.* Premontane Wet Transition to Basal, Wet, and Premontane Rain life zones in Scenario 2) only a small positive effect on TAGC should result (Table 4.3). We hypothesize higher temperature and precipitation will not significantly increase TAGC because greater moisture availability may not compensate the negative effects of higher

temperature on photosynthesis and respiration, even under greater atmospheric CO₂ concentrations (Körner 2003, Würth *et al.* 2005).

In our simulation, the maximum amount of C that secondary forests sequester depends on the C_{max} of each life zone, which decreased over time as the climate and life zones shifted. The area of a life zone that will be occupied by secondary forests also has a strong influence on the amount of C that can be sequestered. For example, C_{max} for Dry and Moist primary forests was 1.4 times greater under current climate than for Scenarios 1 and 2 (Figure 4.2). However, the area of these life zones was up to 6 times greater under the alternative climate scenarios than under current conditions (Table 4.1). Thus, increasing the proportion of a life zone covered by secondary forests resulted in greater secondary forest TAGC under Scenarios 1 and 2 than under current conditions (Table 4.3), even though C_{max} would be lower under the alternative climate scenarios.

Given climate predictions by Campos (1999) and IMN (2000), the most likely future climate for Costa Rica would be one dominated by higher temperature (up to 3.8 °C) and drier conditions (up to 63% reduction in precipitation; *i.e.* more severe drought than in Scenario 1). The degree to which these changes in climate will occur depends on global trends of atmospheric CO₂ concentration and other greenhouse gases (Campos 1999). Regardless of the magnitude of change, it is clear future climate for Costa Rica most likely will continue in the direction of Scenario 1. Under such

conditions, more C would be sequestered by secondary forests growing in life zones with currently lower than average C densities (*i.e.* Dry, Moist, and to a lesser extent Premontane Wet Transition to Basal life zones, Table 4.3) because the areas of these life zones are predicted to increase to up to 6 times their current extent (Table 4.1). The importance of life zones with low carbon densities in maintaining the C balance of Costa Rica increases considering some of the life zones with the highest C densities (*e.g.* Premontane Rain life zone) will disappear under Scenario 1 (Table 4.2, Enquist 2002, IMN 2000).

Secondary forests can play an important role in mitigating impacts of climate change. Under Scenario 1, secondary forests would have to represent a minimum of 19% of the area of a life zone by 2100 (Table 4.3) to offset the C released by primary forest degradation associated with a warmer and drier climate in that same time frame (Figure 4.2). However, if such goal is to be attained, secondary forest regeneration should be promoted in the short term to ensure that secondary forests follow growth trajectories with larger C_{\max} for as long as possible. Competing land uses such as food production and urbanization may prevent attaining this goal in some life zones. For example, anecdotal evidence indicates the area of secondary forests in some Costa Rican regions may no longer be expanding because of increased land pressure from large-scale plantations of pineapple and staple grains, and renewed interest in cattle ranching (Vicente Watson personal communication). In these cases, the promotion of additional secondary forest growth in life zones with lower agricultural potential

should be considered. Management practices that maintain or enhance the capacity of primary and secondary forests to adapt to ongoing climate change should also be considered (Guariguata *et al.* 2008) to minimize losses and maximize C storage in forest ecosystems.

Although our study is restricted to five life zones in Costa Rica, they cover a broad range of climates that occur elsewhere in the tropics. This study offers a reference point to gauge the possible negative effects that climate change may have on C storage in primary forests. In addition, our study serves as a starting point for designing and implementing management strategies that encourage establishment of secondary forests to offset carbon losses from primary forest degradation in Costa Rica and other tropical countries.

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CONCLUSIONS

Tropical secondary forests are often the most wide spread land cover in many tropical regions and may play an important role in mitigating global climate change. In this study we conducted the first comprehensive assessment of total aboveground biomass (TAGB), total aboveground carbon (TAGC), and total ecosystem carbon pools (TEC, including soil C to 1 m depth and root C) in tropical secondary forests in Costa Rica. Our main goal was to quantify the potential of secondary forests growing along a broad tropical climatic gradients (*i.e.* Tropical Dry to Tropical Wet and Premontane forests) to accumulate TAGB and sequester C over time. Our assumption was that, given enough time, secondary forest TAGB, TAGC, and TEC pools would be equivalent to those of primary forests. We originally hypothesized these pools would increase faster and be larger in climates where water is not seasonally limiting to plant growth than in life zones with a distinct dry season. In addition, we examined whether secondary forests have the potential to offset landscape-scale C losses from primary forests under changing climatic conditions expected by the end of the current century.

Trees, the surface layer, and wood debris were the largest components of TAGB. In all life zones, trees represented a greater proportion of TAGB with increasing secondary forest age, ranging across life zones from 7% in secondary forests < 1 yr to 91% of TAGB in older secondary forests. The largest quantities of aboveground biomass in the surface layer were measured in Dry and Moist secondary forests. While the biomass in the surface layer did not change with forest age across life zones, we found that the proportion of TAGB represented was smaller as the age of the secondary

forests increased. We also found older secondary forests in Wetter life zones had greater amounts of downed wood than older forests in the Drier life zones. These data clearly illustrate the changing dynamics of TAGB pools with increasing secondary forest age and highlight the importance of trees as the main storage components of C in secondary forests.

TAGC followed similar trends to those described for TAGB. As expected, TAGC pools were largest in older secondary forests in the Wetter life zones. We found a 28-fold difference in TAGC pools among the sampled secondary forests ranging from 5 $\text{Mg}\cdot\text{ha}^{-1}$ in a 9 yr Dry forest to 143 $\text{Mg}\cdot\text{ha}^{-1}$ in a 60 yr Wet forest. We found secondary forest TAGB was strongly correlated to age and the ratio of potential evapotranspiration to precipitation. In all life zones, TAGC followed a non-linear pattern of sequestration with secondary forest age. In most life zones this pattern was characterized by very rapid growth early in succession, decreasing accumulation rates in mid-succession, and a slow approach to a maximum TAGC similar to that in primary forests. In the Dry life zone, the rapid growth stage was preceded by ~ 14 yr of slow forest growth, possibly caused by limitations to early forest establishment. Mean annual increment (MAI) rates for TAGC accumulation were similar across life zones during the first 20 years of secondary succession. We found a trend of increasing MAI rates of TAGC accumulation with increasing precipitation but differences among life zones were not significant. This provides initial evidence in support of the hypothesis from Guariguata and Ostertag (2001) who predicted Dry

forests would have similar rates of recovery (growth per unit time) of aboveground biomass compared to those found in more humid forests.

We used TAGC from primary forests (Kauffman & Hughes in prep.) to classify the potential of secondary forests to accumulate aboveground C. Life zones fell into three distinct groups. Contrary to our prediction of reduced growth rates resulting in slow TAGC accumulation, secondary forests in the Dry life zone recovered 97% of the TAGC pools in less than 30 years. Despite this fast recovery, but because the maximum expected TAGC pool for forests in this life zone was $73 \text{ Mg}\cdot\text{ha}^{-1}$, we classified Dry secondary forests as having low potential to accumulate TAGC. In comparison, we found secondary forests in the Wet and Premontane Rain life zones, had the highest expected TAGC pools ($207 - 215 \text{ Mg}\cdot\text{ha}^{-1}$). TAGC for these life zones were expected to reach $\geq 90\%$ of TAGC measured in primary forests in > 110 years after pasture abandonment. Finally, we classified secondary forests in the Moist and Premontane Wet life zones as having intermediate TAGC accumulation potential. We estimated they would reach $\geq 90\%$ of TAGC measured in primary forests ($123 - 138 \text{ Mg}\cdot\text{ha}^{-1}$) in $67 - 107$ years after pasture abandonment. Despite the longer recovery times, where accumulating the largest amounts of TAGC is desired as a strategy for mitigation of global climate change, greatest quantities of C per unit area would be found in secondary forests in Wetter life zones. Thus, this is where management efforts (and perhaps economic benefits to the land owner) would most logically be focused.

Our estimates of TAGC of secondary forests growing in the Dry life zone of Costa Rica were higher than those reported elsewhere in the tropics because the former are growing at the wet extreme of the life zone. In contrast, the TAGC we measured in Costa Rican Moist secondary forests were lower than that reported for Moist secondary forests in Brazil (Alves *et al.* 1997, Ferreira & Prance 1999, Steininger 2000b, Uhl *et al.* 1988). However, TAGC we measured compared favorably with that measured in secondary forests growing in oligotrophic conditions in Venezuela and Colombia (Saldarriaga *et al.* 1988), and with sites that had sustained moderate to high intensity of previous land use in Brazil (Fearnside & Guimarães 1996). We suggest long legacies of past land-use in the Moist life zone of Costa Rica (Holdridge 1967) may have reduced the potential of abandoned pasture lands to support highly productive secondary forests.

We offer the first reports of TAGC pools in tropical secondary forests growing in the Premontane Life zone. Comparisons between our data and those from other Montane secondary forests (Fehse *et al.* 2002, Nadkarni *et al.* 2004) suggest Montane secondary forests across the tropics may accumulate similar amounts of TAGC. TAGC pools measured in secondary forests in the remaining life zones of our study were also similar to those reported elsewhere for tropical secondary forests, which supports the adequacy of using our data to assess TAGC accumulation potential by secondary forests in other tropical regions.

Contrary to expectation, we found no changes in soil bulk density (Bd) or soil C concentrations with secondary forest age. Soil Bd was highest in Drier life zones while soil C concentration was highest in the Wetter life zones, and vice versa. Also, while Bd typically increased with soil depth, soil C concentrations decreased with depth. Across all depths, and consistent with worldwide patterns of soil C distribution with climate (Amundson 2001, Post *et al.* 1982), soil C concentrations in Premontane Rain forests was 4 – 6 times greater than in the Dry, Moist, or Premontane Wet – Pacific life zones, and ~ 3 times greater than in the Premontane Wet - Atlantic and Wet life zones.

Soil C to 1 m depth was 1.3 – 2.3 times larger in the Wetter life zones than in the Drier life zones. We found considerable variation in total soil C among sites within the life zones and, contrary to our expectation, were unable to detect changes in soil C as secondary forest aged. The response of soil C to changes in tropical land use from forest to agricultural lands of several types and back to forest is still equivocal. Further studies examining a wider range of secondary forest ages, soil types, and land use categories, combined with the use of stable isotopes (Ehleringer *et al.* 2000) would provide further insights into the dynamics of soil C in tropical secondary forests.

We found significant differences in TEC between life zones, with mean TEC ranging from 149 to 171 Mg·ha⁻¹ in Drier life zones, and between 228 to 370 Mg·ha⁻¹ in Wetter

life zones. Soil C was an important component of TEC pools in secondary forests, ranging from 71 to 79% of TEC across all life zones. Forest age was not a good predictor of TEC across all life zones because of the high variability in soil C pools. Rates of TEC accumulation were lowest in the Dry life zone, increased with increasing precipitation, but reached a maximum and declined at the higher end of our precipitation gradient. We speculate that, while increased water availability can promote forest growth in Dry forests, increased mean annual precipitation may reduce forest productivity by decreasing radiation inputs, increasing nutrient losses, or reducing soil oxygenation (Schuur 2003). We predicted secondary forests would attain $\geq 90\%$ TEC of primary forests in less than 60 yr in the Dry, Moist, and Premontane Wet - Pacific life zones (Table 3.4). In contrast, it would take 62 to 105 yr for secondary forests in the Premontane Wet - Atlantic and Rain life zones to reach TEC equivalent of that in primary forests.

We found a shift in climate to less precipitation and warmer temperature by 2100 had a disproportionate effect in reducing total aboveground carbon of primary forests relative to an increase in both temperature and precipitation. Total aboveground C pools in primary forests growing in five life zones of Costa Rica may decline by up to 65 Tg by the end of the current century. Our simulations suggest this decline may be offset by secondary forest growth. However, at least 19% of the area of each life zone would need to be devoted to secondary forests by 2100 to make this possible. If such goal is to be attained, forest regeneration should be promoted to ensure that secondary

forests are available to sequester C_{\max} for as long as possible. Competing land uses such as food production and urbanization may prevent attaining this goal in some life zones. In these cases, the promotion of additional secondary forest growth in life zones with lower agricultural potential should be considered. Management practices that maintain or enhance the capacity of primary and secondary forests to adapt to ongoing climate change should also be considered (Guariguata *et al.* 2008) to minimize losses and maximize C storage in forest ecosystems.

This is the first study to quantify TAGB, TAGC, and TEC pools of a multitude of secondary forest stands growing along a gradient of tropical climates. Data from this study encompass the necessary variation of tropical climates that would allow calculating the potential of secondary forests to sequester C under changing climatic conditions, and extrapolating those estimates to other tropical areas. However, we caution that before deriving any long-term management recommendations from these data, future climatic variability must be considered because it may affect the potential of secondary forests to sequester C to the levels measured in this study.

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APPENDICES

Appendix A. Basal area ($\text{m}^2 \cdot \text{ha}^{-1}$) by forest component in secondary forests of six life zones in Costa Rica.

Life Zone	Site	Age (yrs)	Palms	Lianas	Herbaceous	Trees (dbh, cm)				Total live	Total dead	Total
						< 10	10-30	30-50	> 50			
Tropical Dry	Pitahaya	9	0.00	0.01	0.00 \pm 0.00	1.07 \pm 0.55	0.03	0.00	0.00	1.12	0.00	1.12
	Bebedero	10	0.00	0.12	0.00 \pm 0.00	7.07 \pm 2.07	3.55	0.00	0.00	10.74	0.13	10.87
	Pocosol	10	0.00	0.01	0.00 \pm 0.00	3.93 \pm 2.64	2.16	0.00	0.00	6.10	0.01	6.11
	Mal Uso	14	0.00	0.21	0.00 \pm 0.00	6.63 \pm 1.59	4.53	0.00	0.00	11.37	0.30	11.67
	Deep Throat	16	0.00	0.45	0.00 \pm 0.00	5.49 \pm 1.76	6.71	0.33	0.00	12.99	0.48	13.47
	Firebreaks	17	0.00	0.00	0.00 \pm 0.00	2.64 \pm 1.15	1.65	0.00	0.00	4.29	0.03	4.32
	Príncipe	22	0.00	0.10	0.00 \pm 0.00	9.04 \pm 2.76	10.97	0.31	0.00	20.43	0.21	20.64
	Naranjo	26	0.00	0.21	0.00 \pm 0.00	3.73 \pm 0.71	7.30	9.83	0.00	21.07	2.38	23.45
	Buen Uso	27	0.00	0.48	0.00 \pm 0.00	6.86 \pm 0.81	13.67	4.78	0.00	25.80	0.94	26.73
	El Pozo	82	0.00	0.62	0.00 \pm 0.00	2.20 \pm 0.41	9.32	7.60	7.29	27.03	1.33	28.36
Tropical Moist	Downey	0.42	1.01	0.02	0.00 \pm 0.00	0.89 \pm 0.39	1.92	0.00	0.00	3.84	4.91	8.74
	Valle Azul	7	1.24	0.30	0.56 \pm 0.37	2.61 \pm 0.94	1.88	0.29	0.00	6.88	0.35	7.23
	Caballos	7	0.06	0.13	0.00 \pm 0.00	5.03 \pm 1.40	7.59	0.58	0.00	13.40	0.10	13.49
	Divino	9	0.00	0.84	0.00 \pm 0.00	6.84 \pm 1.76	6.86	0.00	0.00	14.54	0.29	14.83
	Iguana	13	1.72	0.48	0.20 \pm 0.11	4.24 \pm 1.81	11.70	0.00	0.00	18.34	0.10	18.44
	Quesera	16	0.00	0.36	0.00 \pm 0.00	6.46 \pm 1.72	13.01	0.29	0.00	20.12	1.72	21.84
	Dubya	20	5.32	0.34	0.00 \pm 0.00	2.24 \pm 0.84	9.22	0.00	0.00	17.11	2.03	19.15
	El Tanque	28	0.00	0.77	0.01 \pm 0.01	3.34 \pm 0.85	13.43	0.40	0.00	17.94	7.26	25.20
	Santa Teresa	30	0.59	0.07	0.78 \pm 0.40	0.65 \pm 0.24	10.32	1.43	0.00	13.84	1.81	15.65
	Chonco	40	0.99	0.36	0.00 \pm 0.00	1.88 \pm 0.59	10.40	1.04	0.00	14.67	3.16	17.83
Premontane Wet,	Yucal	2	0.00	0.08	0.00 \pm 0.00	4.96 \pm 0.84	0.40	0.00	0.00	5.44	0.32	5.76
Transition to	Chupadero	6	0.07	0.28	0.00 \pm 0.00	3.43 \pm 0.79	2.06	0.00	0.00	5.83	1.68	7.52
Basal, Pacific	Lapas	10	0.00	0.03	0.01 \pm 0.01	2.21 \pm 0.55	4.67	0.00	0.00	6.93	0.18	7.11
	Hotel	15	0.00	0.15	2.84 \pm 1.47	1.87 \pm 0.70	10.96	3.72	0.00	19.54	0.27	19.81
	Luciano	22	0.00	0.97	0.00 \pm 0.00	6.59 \pm 1.42	8.47	0.00	0.00	16.02	0.02	16.04

Appendix A. (Continued)

Life Zone	Site	Age (yrs)	Palms	Lianas	Herbaceous	Trees (dbh, cm)				Total live	Total dead	Total
						< 10	10-30	30-50	> 50			
Premontane Wet, Transition to Basal, Atlantic	Cano	3	0.00	0.09	0.00 ± 0.00	3.58 ± 1.79	0.73	0.00	0.00	4.41	0.46	4.87
	SAT 900	6	0.00	0.33	0.01 ± 0.01	6.38 ± 1.66	2.96	0.00	0.00	9.68	0.72	10.40
	Con Permiso	10	0.09	0.19	0.00 ± 0.00	6.27 ± 0.84	7.89	0.94	0.00	15.39	7.66	23.05
	SAT 1000	15	0.03	0.71	0.15 ± 0.15	8.56 ± 1.15	6.16	1.99	0.00	17.59	1.84	19.43
	Pao	21	0.63	0.64	0.00 ± 0.00	3.97 ± 0.92	8.66	4.57	1.95	20.43	1.76	22.19
	Cascada	26	0.95	0.31	0.00 ± 0.00	4.87 ± 2.48	12.35	5.46	0.00	23.93	7.36	31.29
	Sábalo	27	0.47	0.30	0.00 ± 0.00	2.81 ± 0.68	6.99	10.13	6.83	27.52	1.70	29.21
	SHO 750	32	0.00	0.12	0.00 ± 0.00	4.25 ± 1.31	9.05	7.63	4.00	25.05	0.86	25.92
Tropical Wet	Terciopelo	0.7	0.00	0.01	0.00 ± 0.00	0.55 ± 0.24	0.00	0.00	0.00	0.56	0.04	0.60
	TUVA	1	0.00	0.07	0.00 ± 0.00	3.22 ± 0.57	0.22	0.00	0.00	3.51	5.56	9.06
	Culebra	3	0.00	0.90	0.00 ± 0.00	2.10 ± 0.84	1.34	0.00	0.00	4.35	5.10	9.45
	La Huerta	6.5	0.00	0.02	0.71 ± 0.27	2.92 ± 0.72	12.44	0.96	0.00	17.04	4.12	21.16
	Don Juan	9	0.18	0.18	0.00 ± 0.00	4.23 ± 0.83	9.48	0.00	0.00	14.07	3.84	17.91
	Tirimbina	18	0.08	0.78	0.00 ± 0.00	4.84 ± 1.49	11.38	0.34	0.00	17.42	2.91	20.33
	Piro	20	0.00	0.07	0.34 ± 0.13	4.69 ± 0.88	5.68	9.37	0.00	20.15	5.36	25.51
	Pumilio	25	0.61	0.33	0.01 ± 0.01	4.72 ± 1.08	13.57	0.74	0.00	19.98	4.55	24.54
	4 Ríos	29	0.74	0.21	0.00 ± 0.00	2.81 ± 1.05	15.68	13.27	0.00	32.71	3.20	35.91
	Caliente	35	1.08	0.27	0.00 ± 0.00	2.56 ± 0.90	11.67	8.04	2.49	26.10	1.25	27.35
	Palma Real	60	0.35	0.25	0.00 ± 0.00	4.93 ± 1.29	11.45	6.41	8.46	31.84	2.95	34.79

Appendix A. (Continued)

Life Zone	Site	Age (yrs)	Palms	Lianas	Herbaceous	Trees (dbh, cm)				Total live	Total dead	Total
						< 10	10-30	30-50	> 50			
Premontane Rain	Volcán	0.5	0.00	0.20	0.00 ± 0.00	1.67 ± 0.62	0.58	0.00	0.00	2.46	0.67	3.12
	Vírgen María	10	0.33	0.23	0.00 ± 0.00	8.87 ± 2.81	7.57	0.00	0.00	16.99	1.52	18.51
	Alemán	15	0.45	0.21	0.95 ± 0.58	5.89 ± 1.87	10.57	0.30	0.00	18.37	1.91	20.28
	Cornelio	19	1.05	0.23	1.05 ± 0.51	6.07 ± 1.25	15.11	3.00	0.00	26.51	1.72	28.23
	Milpa	20	0.40	0.47	1.30 ± 0.70	3.49 ± 1.22	8.82	4.69	0.79	19.97	6.69	26.67
	Dos Ases	20	1.93	0.21	0.00 ± 0.00	3.84 ± 0.84	6.56	12.93	0.00	25.46	3.68	29.14
	Cambronero	30	0.16	0.49	0.62 ± 0.37	3.24 ± 0.84	7.41	14.60	0.00	26.53	4.33	30.86
	Hondura	35	0.00	0.16	0.00 ± 0.00	3.90 ± 1.09	10.08	6.96	3.29	24.38	4.63	29.01
	Vargas	40	0.84	0.13	0.93 ± 0.63	3.85 ± 1.60	10.84	16.40	1.67	34.66	3.52	38.17
	Kraven S.A.	50	1.35	0.77	0.31 ± 0.31	6.24 ± 1.62	13.12	8.63	1.73	32.17	14.35	46.52

Notes: Mean ± SE is provided for forest components subsampled within each 50 x 50 m plot, not for components that include whole plot measures. Tree basal area is categorized by "diameter at breast height" (dbh) classes (cm); dbh was measured at 1.3 m height. Total Dead includes basal area of small dead stems dbh < 10 cm, and snags dbh > 10 cm. Total Live includes all other categories. Total is the sum of basal area of all forest components.

Appendix B. Stem density (stems·ha⁻¹) by forest component in secondary forests of six life zones in Costa Rica.

Life Zone	Site	Age (yrs)	Palms	Lianas	Herbaceous	Trees (dbh, cm)				Trees >10	Total live	Total dead	Total
						< 10	10-30	30-50	> 50				
Tropical Dry	Pitahaya	9	0	667	0 ± 0	4083 ± 1591	4	0	0	4	4754	0	4754
	Bebedero	10	0	1417	0 ± 0	10500 ± 2701	296	0	0	296	12213	504	12717
	Pocosol	10	0	500	0 ± 0	8167 ± 2822	136	0	0	136	8803	667	9469
	Mal Uso	14	0	3917	0 ± 0	6000 ± 1517	344	0	0	344	10261	500	10761
	Deep Throat	16	0	10667	0 ± 0	6583 ± 1616	404	4	0	408	17658	1254	18912
	Firebreaks	17	0	83	0 ± 0	3833 ± 1511	108	0	0	108	4025	500	4525
	Príncipe	22	0	2667	0 ± 0	8417 ± 1512	756	4	0	760	11843	91	11935
	Naranjo	26	0	3917	0 ± 0	3500 ± 784	276	92	0	368	7785	873	8658
	Buen Uso	27	0	4583	0 ± 0	5083 ± 796	592	48	0	640	10307	449	10755
	El Pozo	82	0	2333	0 ± 0	3167 ± 1052	360	72	24	456	5956	187	6143
Tropical Moist	Downey	0.42	16	2750	0 ± 0	12750 ± 2151	44	0	0	44	15560	48	15608
	Valle Azul	7	250	10500	1083 ± 666	6833 ± 1302	108	4	0	112	18779	3500	22279
	Caballos	7	4	9583	0 ± 0	13583 ± 1804	368	8	0	376	23547	1917	25463
	Divino	9	0	16083	0 ± 0	10083 ± 2223	520	0	0	520	26687	921	27607
	Iguana	13	48	4583	500 ± 327	4833 ± 1893	552	0	0	552	10517	333	10850
	Quesera	16	0	7917	0 ± 0	5667 ± 1339	756	4	0	760	14343	1877	16221
	Dubya	20	6913	6250	0 ± 0	6583 ± 1482	572	0	0	572	20319	2365	22684
	El Tanque	28	0	7845	83 ± 83	17750 ± 5578	604	4	0	608	26287	6719	33005
	Santa Teresa	30	254	2417	1500 ± 467	8083 ± 2473	468	16	0	484	12738	1143	13881
	Chonco	40	4750	8417	0 ± 0	4750 ± 979	412	12	0	424	18341	831	19171
Premontane Wet, Transition to Basal, Pacific	Yucal	2	0	9000	0 ± 0	5750 ± 845	32	0	0	32	14782	1083	15865
	Chupadero	6	167	6250	0 ± 0	5250 ± 1250	164	0	0	164	11831	258	12089
	Lapas	10	0	7500	83 ± 83	5833 ± 1296	328	0	0	328	13745	758	14503
	Hotel	15	0	4083	8917 ± 5671	3583 ± 908	424	40	0	464	17047	20	17067
	Luciano	22	0	7167	0 ± 0	4583 ± 1042	524	0	0	524	12274	167	12441

Appendix B. (Continued)

Life Zone	Site	Age (yrs)	Palms	Lianas	Herbaceous	Trees (dbh, cm)				Trees >10	Total live	Total	
						< 10	10-30	30-50	> 50			dead	Total
Premontane Wet,	Cano	3	0	1583	0 ± 0	10000 ± 2817	60	0	0	60	11643	504	12147
Transition to	SAT 900	6	0	7417	1000 ± 826	12583 ± 1620	168	0	0	168	21168	24	21192
Basal, Atlantic	Con Permiso	10	4	6000	0 ± 0	9917 ± 1019	408	12	0	420	16341	885	17226
	SAT 1000	15	4	12671	167 ± 167	12250 ± 1598	292	24	0	316	25407	1036	26443
	Pao	21	449	12921	0 ± 0	7083 ± 908	324	40	8	372	20825	643	21468
	Cascada	26	195	10583	0 ± 0	6750 ± 684	508	56	0	564	18092	417	18509
	Sábalo	27	179	11167	0 ± 0	5083 ± 745	288	92	28	408	16837	536	17373
	SHO 750	32	0	7000	0 ± 0	9583 ± 1628	392	60	16	468	17051	762	17813
Tropical Wet	Terciopelo	0.7	0	1000	0 ± 0	4833 ± 1567	0	0	0	0	5833	83	5917
	TUVA	1	0	11250	0 ± 0	25250 ± 5203	8	0	0	8	36508	1052	37560
	Culebra	3	0	16583	0 ± 0	15333 ± 6671	64	0	0	64	31981	20	32001
	La Huerta	6.5	0	1500	2000 ± 667	8833 ± 880	524	12	0	536	12869	652	13521
	Don Juan	9	12	4833	0 ± 0	9750 ± 1038	376	0	0	376	14971	405	15377
	Tirimbina	18	4	35083	0 ± 0	12917 ± 3114	464	4	0	468	48472	544	49016
	Piro	20	0	2000	750 ± 265	21000 ± 2726	208	80	0	288	24038	1473	25511
	Pumilio	25	333	7917	83 ± 83	7833 ± 1097	640	8	0	648	16815	711	17526
	4 Ríos	29	306	13833	0 ± 0	8167 ± 2210	520	108	0	628	22934	409	23343
	Caliente	35	425	2250	0 ± 0	5000 ± 1222	408	68	12	488	8163	40	8203
	Palma Real	60	1175	3417	0 ± 0	9250 ± 1477	448	52	32	532	14373	377	14751

Appendix B. (Continued)

Life Zone	Site	Age (yrs)	Palms	Lianas	Herbaceous	Trees (dbh, cm)				Trees >10	Total live	Total dead	Total
						< 10	10-30	30-50	> 50				
Premontane Rain	Volcán	0.5	0	18933	0 ± 0	14000 ± 2996	16	0	0	16	32949	145	33095
	Virgen María	10	12	7171	0 ± 0	10417 ± 2839	460	0	0	460	18059	1099	19159
	Alemán	15	36	11167	417 ± 250	12000 ± 3392	592	4	0	596	24215	1628	25843
	Cornelio	19	457	6417	500 ± 209	17750 ± 3436	560	32	0	592	25715	326	26041
	Milpa	20	24	7417	3167 ± 1694	11417 ± 2018	364	36	4	404	22428	425	22853
	Dos Ases	20	104	8417	0 ± 0	15083 ± 3259	260	116	0	376	23980	806	24786
	Cambronero	30	12	15250	417 ± 175	15917 ± 2198	372	124	0	496	32091	715	32806
	Hondura	35	0	10083	0 ± 0	9833 ± 1708	472	64	12	548	20465	707	21172
	Vargas	40	52	9250	167 ± 109	7667 ± 1548	460	140	8	608	17743	389	18133
	Kraven S.A.	50	219	23250	83 ± 83	9750 ± 1773	560	80	8	648	33950	822	34772

Notes: Mean ± SE is provided for ecosystem components subsampled within each 50 x 50 m plot, not for components that include whole plot measures. Stem density for all stems with height > 1.30 m. Stem density of dead stems includes stems dbh < 10 cm, and snags dbh > 10 cm. Stem density of total live stems includes all other categories. Total is the sum of stem density of all forest components.

Appendix C. Aboveground carbon pools ($\text{Mg}\cdot\text{ha}^{-1}$) by ecosystem component in secondary forests of six life zones of Costa Rica. Values are mean \pm SE.

Life Zone	Site name	Age	Wood debris	Surface layer	Palms	Lianas	Herbaceous	Trees (dbh, cm)				Total live	Total dead	TAGC
								< 10	10-30	30-50	> 50			
Tropical Dry	Pitahaya	9	0.00 \pm 0.00	3.86 \pm 0.71	0.00	0.07	0.00 \pm 0.00	1.12 \pm 0.58	0.04	0.00	0.00	5.09	0.00	5.09
	Bebedero	10	0.26 \pm 0.15	4.99 \pm 0.92	0.00	0.79	0.00 \pm 0.00	7.55 \pm 2.25	6.61	0.00	0.00	19.94	0.34	20.28
	Pocosol	10	0.00 \pm 0.00	3.88 \pm 0.79	0.00	0.04	0.00 \pm 0.00	4.30 \pm 2.92	4.75	0.00	0.00	12.96	0.01	12.96
	Mal Uso	14	0.75 \pm 0.35	5.42 \pm 1.03	0.00	1.37	0.00 \pm 0.00	7.33 \pm 1.78	8.35	0.00	0.00	22.47	1.03	23.49
	Deep Throat	16	0.20 \pm 0.08	5.03 \pm 1.00	0.00	3.12	0.00 \pm 0.00	6.10 \pm 1.98	14.93	0.69	0.00	29.88	0.63	30.51
	Firebreaks	17	0.15 \pm 0.10	3.14 \pm 0.54	0.00	0.00	0.00 \pm 0.00	2.96 \pm 1.31	3.23	0.00	0.00	9.34	0.17	9.51
	Príncipe	22	0.18 \pm 0.08	6.06 \pm 0.53	0.00	0.66	0.00 \pm 0.00	10.13 \pm 3.12	22.91	0.45	0.00	40.22	0.26	40.48
	Naranjo	26	5.56 \pm 1.69	4.99 \pm 1.40	0.00	1.52	0.00 \pm 0.00	4.11 \pm 0.79	16.55	24.27	0.00	51.43	6.69	58.12
	Buen Uso	27	3.25 \pm 0.89	7.16 \pm 2.10	0.00	3.55	0.00 \pm 0.00	7.65 \pm 0.92	37.41	10.63	0.00	66.39	3.52	69.90
	El Pozo	82	4.03 \pm 1.47	3.99 \pm 0.56	0.00	4.71	0.00 \pm 0.00	2.36 \pm 0.44	18.45	18.40	21.87	69.78	4.18	73.96
Tropical Moist	Downey	0.42	3.99 \pm 1.64	4.21 \pm 0.51	0.22	0.10	0.00 \pm 0.00	0.90 \pm 0.43	5.03	0.00	0.00	10.46	4.02	14.48
	Valle Azul	7	0.22 \pm 0.09	2.97 \pm 0.21	0.22	1.91	0.33 \pm 0.20	2.79 \pm 1.06	4.62	1.01	0.00	13.84	0.77	14.62
	Caballos	7	1.19 \pm 0.28	3.43 \pm 0.36	0.03	0.79	0.00 \pm 0.00	5.41 \pm 1.59	19.48	1.99	0.00	31.12	1.26	32.39
	Divino	9	0.74 \pm 0.21	2.37 \pm 0.40	0.00	5.89	0.00 \pm 0.00	7.63 \pm 2.00	15.49	0.00	0.00	31.38	0.99	32.37
	Iguana	13	0.74 \pm 0.22	3.62 \pm 0.35	2.22	3.38	0.04 \pm 0.03	4.79 \pm 2.08	29.79	0.00	0.00	43.83	0.82	44.65
	Quesera	16	1.99 \pm 0.43	3.69 \pm 0.28	0.00	2.40	0.00 \pm 0.00	7.20 \pm 1.95	35.61	1.00	0.00	49.90	4.36	54.26
	Dubya	20	0.94 \pm 0.34	5.09 \pm 0.81	4.46	2.36	0.00 \pm 0.00	2.41 \pm 0.96	21.98	0.00	0.00	36.30	1.53	37.83
	El Tanque	28	2.16 \pm 0.42	3.24 \pm 0.71	0.00	5.69	0.03 \pm 0.03	3.53 \pm 0.89	35.21	0.95	0.00	48.65	2.42	51.08
	Santa Teresa	30	1.71 \pm 0.38	3.20 \pm 0.35	0.32	0.42	0.37 \pm 0.12	0.63 \pm 0.24	25.06	4.34	0.00	34.34	2.72	37.06
	Chonco	40	1.62 \pm 0.43	3.38 \pm 0.44	0.75	2.35	0.00 \pm 0.00	2.05 \pm 0.67	28.66	3.02	0.00	40.21	1.70	41.91
Premontane Wet,	Yucal	2	0.80 \pm 0.77	2.03 \pm 0.40	0.00	0.46	0.00 \pm 0.00	5.43 \pm 0.92	0.63	0.00	0.00	8.56	1.10	9.65
Transition to Basal,	Chupadero	6	1.04 \pm 0.50	2.61 \pm 0.43	0.12	1.85	0.00 \pm 0.00	3.79 \pm 0.90	4.41	0.00	0.00	12.78	1.83	14.61
Pacific	Lapas	10	0.28 \pm 0.10	1.52 \pm 0.14	0.00	0.15	0.04 \pm 0.04	2.35 \pm 0.63	10.18	0.00	0.00	14.24	0.39	14.62
	Hotel	15	0.86 \pm 0.31	3.59 \pm 0.82	0.00	1.01	2.28 \pm 1.61	2.03 \pm 0.78	28.13	12.57	0.00	49.61	1.01	50.61
	Luciano	22	0.31 \pm 0.08	2.53 \pm 0.30	0.00	7.13	0.00 \pm 0.00	7.64 \pm 1.66	18.41	0.00	0.00	35.70	0.44	36.14

Appendix C. (Continued)

Life Zone	Site name	Age	Wood debris	Surface layer	Palms	Lianas	Herbaceous	Trees (dbh, cm)				Total live	Total dead	TAGC
								< 10	10-30	30-50	> 50			
Premontane Wet,	Cano	3	1.32 ± 0.46	3.57 ± 0.44	0.00	0.54	0.00 ± 0.00	3.69 ± 1.95	1.47	0.00	0.00	9.27	1.71	10.98
Transition to Basal,	SAT 900	6	1.00 ± 0.42	2.67 ± 0.50	0.00	1.97	0.14 ± 0.12	6.63 ± 1.74	6.82	0.00	0.00	18.24	1.01	19.25
Atlantic	Con Permiso	10	11.23 ± 3.92	2.84 ± 0.56	0.16	1.17	0.00 ± 0.00	6.54 ± 0.89	18.37	1.83	0.00	30.89	11.84	42.74
	SAT 1000	15	5.25 ± 1.10	2.28 ± 0.41	0.08	4.32	0.02 ± 0.02	8.78 ± 1.20	15.22	5.59	0.00	36.29	5.55	41.84
	Pao	21	12.71 ± 2.31	2.96 ± 0.68	1.63	3.91	0.00 ± 0.00	4.16 ± 1.01	23.18	12.90	5.00	53.74	13.23	66.97
	Cascada	26	6.18 ± 1.57	2.32 ± 0.21	2.07	1.99	0.00 ± 0.00	5.15 ± 2.73	36.52	18.37	0.00	66.41	6.25	72.66
	Sábalo	27	12.99 ± 3.66	2.44 ± 0.32	0.84	2.01	0.00 ± 0.00	2.84 ± 0.71	18.31	34.02	21.35	81.81	13.12	94.93
	SHO 750	32	5.58 ± 1.95	2.14 ± 0.18	0.00	0.85	0.00 ± 0.00	4.45 ± 1.41	24.72	22.83	12.20	67.20	6.23	73.43
Tropical Wet	Terciopelo	0.7	0.39 ± 0.24	6.98 ± 0.73	0.00	0.06	0.00 ± 0.00	0.52 ± 0.23	0.00	0.00	0.00	7.55	0.42	7.98
	TUVA	1	1.32 ± 0.53	2.61 ± 0.38	0.00	0.52	0.00 ± 0.00	2.97 ± 0.52	0.48	0.00	0.00	6.59	1.55	8.14
	Culebra	3	3.05 ± 1.03	6.13 ± 0.78	0.00	4.80	0.00 ± 0.00	2.00 ± 0.81	3.47	0.00	0.00	16.39	3.07	19.46
	La Huerta	6.5	8.07 ± 1.83	2.77 ± 0.42	0.00	0.12	0.29 ± 0.11	2.95 ± 0.77	22.86	1.34	0.00	30.33	9.88	40.21
	Don Juan	9	5.32 ± 2.28	2.14 ± 0.42	0.48	1.05	0.00 ± 0.00	4.37 ± 0.91	26.55	0.00	0.00	34.59	5.36	39.95
	Tirimbina	18	8.18 ± 1.54	2.22 ± 0.21	0.11	5.06	0.00 ± 0.00	4.92 ± 1.54	33.38	1.57	0.00	47.26	9.17	56.43
	Piro	20	2.01 ± 0.38	2.00 ± 0.33	0.00	0.43	0.15 ± 0.06	4.67 ± 0.97	14.95	34.78	0.00	56.98	4.89	61.87
	Pumilio	25	14.28 ± 2.54	3.24 ± 0.44	0.96	2.03	0.01 ± 0.01	4.96 ± 1.18	36.36	3.01	0.00	50.57	14.61	65.18
	4 Ríos	29	2.73 ± 0.38	2.70 ± 0.34	2.46	1.47	0.00 ± 0.00	2.89 ± 1.12	52.19	52.97	0.00	114.69	3.46	118.15
	Caliente	35	5.90 ± 1.64	3.75 ± 0.50	0.53	1.37	0.00 ± 0.00	2.68 ± 0.99	29.47	29.49	9.18	76.46	5.91	82.37
	Palma Real	60	27.25 ± 13.13	2.18 ± 0.31	0.60	1.48	0.00 ± 0.00	5.14 ± 1.43	42.01	25.94	38.37	115.74	27.35	143.08

Appendix C. (Continued)

Life Zone	Site name	Age	Wood debris	Surface layer	Palms	Lianas	Herbaceous	Trees (dbh, cm)				Total live	Total dead	Total TAGC
								< 10	10-30	30-50	> 50			
Premontane Rain	Volcán	0.5	1.50 ± 0.81	1.80 ± 1.02	0.00	1.49	0.00 ± 0.00	1.57 ± 0.60	1.60	0.00	0.00	6.46	1.51	7.97
	Virgen María	10	2.72 ± 0.90	2.35 ± 0.35	0.50	1.41	0.00 ± 0.00	9.26 ± 2.96	20.41	0.00	0.00	33.93	3.08	37.01
	Alemán	15	1.45 ± 0.66	2.70 ± 0.31	0.39	1.40	1.31 ± 0.83	6.34 ± 2.15	34.38	1.02	0.00	47.55	1.66	49.22
	Cornelio	19	5.94 ± 1.94	2.51 ± 0.29	1.55	1.41	1.49 ± 0.76	6.20 ± 1.32	52.47	13.03	0.00	78.66	6.04	84.70
	Milpa	20	11.66 ± 2.76	3.58 ± 0.54	0.61	2.54	0.31 ± 0.17	3.67 ± 1.36	26.67	15.91	2.96	56.25	11.93	68.18
	Dos Ases	20	8.45 ± 1.91	4.05 ± 0.69	2.25	1.36	0.00 ± 0.00	3.94 ± 0.91	22.54	54.48	0.00	88.63	8.95	97.58
	Cambrónero	30	5.14 ± 1.32	3.85 ± 0.66	0.25	2.80	0.88 ± 0.55	3.32 ± 0.93	19.18	56.95	0.00	87.22	5.93	93.15
	Hondura	35	7.67 ± 1.96	5.99 ± 1.08	0.00	1.12	0.00 ± 0.00	4.13 ± 1.19	29.21	24.91	14.58	79.94	8.67	88.61
	Vargas	40	4.74 ± 1.19	3.38 ± 0.15	1.13	0.88	1.32 ± 0.89	4.18 ± 1.81	29.07	66.35	6.43	112.74	4.78	117.53
	Kraven S.A.	50	17.83 ± 4.59	3.28 ± 0.63	1.65	4.80	0.46 ± 0.46	6.59 ± 1.76	37.61	29.62	6.15	90.16	18.14	108.30

Notes: Mean ± SE is provided for ecosystem components subsampled within each 50 x 50 m plot, not for components that include whole plot measures. Surface Layer includes litter and seedlings and is considered part of Total Live. Mass of C in Trees is categorized by diameter (dbh) classes (cm); dbh was measured at 1.3 m height. Total Dead includes wood debris, small dead stems dbh < 10 cm, and snags dbh > 10 cm. Total Live includes all other categories. Total Above Ground C (TAGC) is the sum of all aboveground carbon pools.

Appendix D. Soil bulk density ($\text{g}\cdot\text{cm}^{-3}$) of secondary forests growing in six life zones of Costa Rica. Values are mean \pm SE.

Life Zone	Site name	Age (yrs)	Depth interval (cm)				
			0-10	10-20	20-30	30-50	50-100
Tropical Dry	Pitahaya	9	1.15 \pm 0.07	1.44 \pm 0.10	1.47 \pm 0.07	1.63 \pm 0.03	1.46 \pm 0.03
	Bebedero	15	1.32 \pm 0.04	1.42 \pm 0.09	1.53 \pm 0.11	1.55 \pm 0.09	n.c.
	Pocosol	15	1.40 \pm 0.02	1.37 \pm 0.10	1.41 \pm n.a.	n.c.	n.c.
	Mal Uso	14	1.33 \pm 0.05	1.30 \pm 0.04	1.31 \pm 0.05	1.50 \pm 0.07	1.48 \pm n.a.
	Deep Throat	16	1.26 \pm 0.04	1.31 \pm 0.04	1.30 \pm 0.10	1.46 \pm 0.11	1.51 \pm 0.02
	Firebreaks	17	1.28 \pm 0.10	1.39 \pm 0.23	1.23 \pm 0.07	1.53 \pm 0.10	n.c.
	Príncipe	22	1.19 \pm 0.06	1.26 \pm 0.07	1.43 \pm 0.10	1.51 \pm 0.17	n.c.
	Naranjo	26	1.13 \pm 0.05	1.21 \pm 0.03	1.26 \pm 0.04	1.37 \pm 0.02	1.32 \pm 0.05
	Buen Uso	27	1.25 \pm 0.05	1.21 \pm 0.07	1.39 \pm 0.03	1.31 \pm 0.11	1.34 \pm 0.04
	El Pozo	82	1.57 \pm 0.16	1.47 \pm 0.16	1.58 \pm 0.19	1.38 \pm 0.13	1.48 \pm 0.17
Tropical Moist	Downey	0.42	1.28 \pm 0.03	1.38 \pm 0.09	1.26 \pm 0.05	1.35 \pm 0.05	1.32 \pm 0.05
	Valle Azul	7	1.57 \pm 0.03	1.36 \pm 0.01	1.35 \pm 0.02	1.40 \pm 0.06	1.53 \pm 0.05
	Caballos	7	1.40 \pm 0.03	1.30 \pm 0.06	1.24 \pm 0.07	1.46 \pm 0.04	1.52 \pm 0.10
	Divino	9	1.47 \pm 0.06	1.39 \pm 0.08	1.29 \pm 0.06	1.41 \pm 0.09	1.38 \pm 0.06
	Iguana	13	1.24 \pm 0.07	1.32 \pm 0.09	1.37 \pm 0.06	1.37 \pm 0.04	1.28 \pm 0.05
	Quesera	16	1.09 \pm 0.07	1.20 \pm 0.03	1.22 \pm 0.10	1.46 \pm 0.25	n.c.
	Dubya	20	1.35 \pm 0.04	1.52 \pm 0.09	1.30 \pm 0.05	1.42 \pm 0.06	1.42 \pm 0.12
	El Tanque	28	1.35 \pm 0.02	1.34 \pm 0.04	1.27 \pm 0.05	1.38 \pm 0.10	1.43 \pm 0.06
	Santa Teresa	30	1.25 \pm 0.06	1.31 \pm 0.09	1.39 \pm 0.04	1.28 \pm 0.07	1.45 \pm 0.07
	Chonco	40	1.33 \pm 0.12	1.35 \pm 0.02	1.34 \pm 0.06	1.45 \pm 0.05	1.46 \pm 0.06
Premontane Wet, Transition to Basal, Pacific	Yucal	2	1.29 \pm 0.08	1.21 \pm 0.08	1.31 \pm 0.10	1.36 \pm 0.06	1.35 \pm 0.04
	Chupadero	6	1.36 \pm 0.04	1.31 \pm 0.05	1.30 \pm 0.04	1.42 \pm 0.09	1.49 \pm 0.04
	Lapas	10	1.41 \pm 0.04	1.42 \pm 0.06	1.47 \pm 0.05	1.54 \pm 0.07	1.46 \pm 0.06
	Hotel	15	1.37 \pm 0.04	1.25 \pm 0.05	1.32 \pm 0.07	1.30 \pm 0.05	1.45 \pm 0.08
	Luciano	22	1.18 \pm 0.05	1.23 \pm 0.04	1.16 \pm 0.03	1.29 \pm 0.03	1.38 \pm 0.08
Premontane Wet, Transition to Basal, Atlantic	Cano	3	0.87 \pm 0.03	1.03 \pm 0.04	0.91 \pm 0.05	0.98 \pm 0.02	1.00 \pm 0.04
	SAT 900	6	0.91 \pm 0.05	1.00 \pm 0.01	1.01 \pm 0.02	1.07 \pm 0.05	1.11 \pm 0.03
	Con Permiso	10	0.85 \pm 0.03	0.88 \pm 0.03	0.94 \pm 0.01	0.90 \pm 0.03	0.93 \pm 0.02
	SAT 1000	15	0.97 \pm 0.04	1.13 \pm 0.01	1.11 \pm 0.04	1.09 \pm 0.05	1.05 \pm 0.02
	Pao	21	0.89 \pm 0.03	1.02 \pm 0.02	1.01 \pm 0.02	1.02 \pm 0.03	1.05 \pm 0.02
	Cascada	26	0.96 \pm 0.13	0.91 \pm 0.05	1.02 \pm 0.06	1.00 \pm 0.04	1.05 \pm 0.04
	Sábalo	27	0.90 \pm 0.03	0.94 \pm 0.03	1.01 \pm 0.01	1.07 \pm 0.02	1.07 \pm 0.01
	SHO 750	32	0.77 \pm 0.04	0.88 \pm 0.03	0.90 \pm 0.02	1.00 \pm 0.02	0.99 \pm 0.01
Tropical Wet	Terciopelo	0.7	1.03 \pm 0.05	0.94 \pm 0.07	0.87 \pm 0.05	1.05 \pm 0.01	1.11 \pm 0.03
	TUVA	1	1.26 \pm 0.06	1.24 \pm 0.06	1.28 \pm 0.04	1.30 \pm 0.06	1.27 \pm 0.06
	Culebra	3	1.00 \pm 0.06	1.00 \pm 0.01	0.96 \pm 0.06	1.07 \pm 0.07	1.09 \pm 0.05
	La Huerta	6.5	1.16 \pm 0.05	1.19 \pm 0.07	1.17 \pm 0.06	1.19 \pm 0.02	1.20 \pm 0.06
	Don Juan	9	0.79 \pm 0.03	0.87 \pm 0.03	0.92 \pm 0.03	1.00 \pm 0.03	1.01 \pm 0.04
	Tirimina	18	0.88 \pm 0.05	1.00 \pm 0.03	1.05 \pm 0.02	1.04 \pm 0.02	1.03 \pm 0.02
	Piro	20	1.16 \pm 0.07	1.35 \pm 0.07	1.30 \pm 0.06	1.34 \pm 0.02	1.30 \pm 0.04
	Pumilio	25	0.78 \pm 0.03	0.86 \pm 0.02	0.91 \pm 0.03	1.01 \pm 0.02	0.98 \pm 0.02
	4 Ríos	29	0.90 \pm 0.03	1.01 \pm 0.01	1.01 \pm 0.02	1.10 \pm 0.03	1.06 \pm 0.05
	Caliente	35	1.17 \pm 0.06	1.23 \pm 0.03	1.22 \pm 0.05	1.40 \pm 0.04	1.29 \pm 0.08
	Palma Real	60	1.17 \pm 0.09	1.29 \pm 0.03	1.27 \pm 0.08	1.44 \pm 0.02	1.38 \pm 0.05

Appendix D. (Continued)

Life Zone	Site name	Age (yrs)	Depth interval (cm)				
			0-10	10-20	20-30	30-50	50-100
Premontane Rain	Volcán	0.5	0.60 ± 0.05	0.66 ± 0.06	0.66 ± 0.07	0.67 ± 0.07	0.85 ± 0.06
	Vírgen María	10	0.48 ± 0.04	0.49 ± 0.06	0.47 ± 0.02	0.58 ± 0.03	0.64 ± 0.05
	Alemán	15	0.32 ± 0.03	0.43 ± 0.03	0.46 ± 0.04	0.52 ± 0.03	0.50 ± 0.03
	Cornelio	19	0.42 ± 0.05	0.47 ± 0.04	0.54 ± 0.04	0.60 ± 0.03	0.57 ± 0.03
	Milpa	20	0.40 ± 0.01	0.46 ± 0.02	0.44 ± 0.02	0.52 ± 0.02	0.73 ± 0.05
	Dos Ases	20	0.36 ± 0.04	0.50 ± 0.04	0.54 ± 0.07	0.74 ± 0.06	0.67 ± 0.09
	Cambroneró	30	0.37 ± 0.04	0.56 ± 0.10	0.64 ± 0.07	0.72 ± 0.05	0.54 ± 0.06
	Hondura	35	0.47 ± 0.02	0.45 ± 0.03	0.49 ± 0.01	0.61 ± 0.04	0.62 ± 0.05
	Vargas	40	0.33 ± 0.04	0.52 ± 0.02	0.53 ± 0.04	0.62 ± 0.05	0.54 ± 0.04
	Kraven S.A.	50	0.40 ± 0.02	0.40 ± 0.02	0.43 ± 0.01	0.56 ± 0.04	0.72 ± 0.08

Notes: "n.c" indicates samples were not collected; "n.a." indicates insufficient data to calculate SE.

Appendix E. Soil carbon concentration (%) of secondary forests growing in six life zones of Costa Rica. Values are mean \pm SE.

Life Zone	Site name	Age (yrs)	Depth interval (cm)				
			0-10	10-20	20-30	30-50	50-100
Tropical Dry	Pitahaya	9	2.93 \pm 0.19	1.49 \pm 0.12	0.95 \pm 0.07	0.74 \pm 0.04	0.78 \pm 0.01
	Bebedero	15	3.04 \pm 0.12	1.84 \pm 0.12	0.92 \pm 0.06	0.89 \pm 0.04	n.c.
	Pocosol	15	3.19 \pm 0.21	2.04 \pm 0.13	1.55 \pm n.a.	n.c.	n.c.
	Mal Uso	14	4.07 \pm 0.19	2.38 \pm 0.05	1.88 \pm 0.05	1.44 \pm 0.06	1.09 \pm n.a.
	Deep Throat	16	4.58 \pm 0.35	2.76 \pm 0.12	2.12 \pm 0.22	1.48 \pm 0.13	1.19 \pm 0.16
	Firebreaks	17	2.88 \pm 0.43	1.48 \pm 0.15	0.95 \pm 0.10	0.70 \pm 0.08	n.c.
	Príncipe	22	4.12 \pm 0.50	2.45 \pm 0.47	1.51 \pm 0.25	1.16 \pm 0.17	n.c.
	Naranjo	26	5.08 \pm 0.81	2.24 \pm 0.37	2.22 \pm 0.17	1.56 \pm 0.18	0.78 \pm 0.05
	Buen Uso	27	4.00 \pm 0.28	2.48 \pm 0.07	1.74 \pm 0.10	1.26 \pm 0.04	0.84 \pm 0.11
	El Pozo	82	3.81 \pm 0.43	2.50 \pm 0.11	2.05 \pm 0.08	1.23 \pm 0.14	0.83 \pm 0.10
Tropical Moist	Downey	0.42	4.39 \pm 0.57	2.10 \pm 0.16	1.24 \pm 0.18	0.79 \pm 0.05	0.50 \pm 0.08
	Valle Azul	7	1.64 \pm 0.09	1.00 \pm 0.07	0.64 \pm 0.03	0.31 \pm 0.03	0.25 \pm 0.06
	Caballos	7	5.14 \pm 0.79	2.67 \pm 0.10	1.91 \pm 0.18	1.31 \pm 0.13	1.12 \pm 0.23
	Divino	9	2.39 \pm 0.05	1.63 \pm 0.15	1.02 \pm 0.13	0.51 \pm 0.07	0.31 \pm 0.04
	Iguana	13	4.26 \pm 0.22	2.67 \pm 0.12	1.39 \pm 0.15	1.08 \pm 0.07	0.92 \pm 0.20
	Quesera	16	4.10 \pm 0.58	3.18 \pm 0.72	3.00 \pm 0.99	1.26 \pm 0.01	n.c.
	Dubya	20	4.02 \pm 0.34	2.36 \pm 0.23	1.58 \pm 0.17	0.98 \pm 0.07	0.73 \pm 0.07
	El Tanque	28	1.98 \pm 0.55	1.51 \pm 0.29	1.04 \pm 0.19	0.82 \pm 0.20	0.57 \pm 0.17
	Santa Teresa	30	3.12 \pm 0.25	1.62 \pm 0.06	1.07 \pm 0.14	0.91 \pm 0.16	0.38 \pm 0.10
	Chonco	40	3.32 \pm 0.38	2.15 \pm 0.22	1.63 \pm 0.21	0.97 \pm 0.15	0.51 \pm 0.12
Premontane Wet, Transition to Basal, Pacific	Yucal	2	3.43 \pm 0.40	2.58 \pm 0.15	2.31 \pm 0.19	1.76 \pm 0.23	1.16 \pm 0.35
	Chupadero	6	2.76 \pm 0.22	1.71 \pm 0.19	1.39 \pm 0.17	0.79 \pm 0.20	0.42 \pm 0.06
	Lapas	10	2.54 \pm 0.13	1.51 \pm 0.10	1.02 \pm 0.14	0.55 \pm 0.08	0.38 \pm 0.07
	Hotel	15	1.74 \pm 0.27	1.34 \pm 0.10	0.71 \pm 0.05	0.67 \pm 0.12	0.64 \pm 0.11
	Luciano	22	3.18 \pm 0.35	1.72 \pm 0.13	1.12 \pm 0.13	0.71 \pm 0.13	0.42 \pm 0.07
Premontane Wet, Transition to Basal, Atlantic	Cano	3	5.66 \pm 0.24	3.51 \pm 0.22	2.54 \pm 0.24	1.89 \pm 0.19	1.30 \pm 0.15
	SAT 900	6	4.83 \pm 0.55	3.10 \pm 0.24	2.21 \pm 0.15	1.50 \pm 0.08	0.85 \pm 0.08
	Con Permiso	10	7.02 \pm 0.41	4.16 \pm 0.45	2.76 \pm 0.20	1.72 \pm 0.04	1.18 \pm 0.05
	SAT 1000	15	4.41 \pm 0.74	2.63 \pm 0.09	1.75 \pm 0.07	1.42 \pm 0.06	1.01 \pm 0.08
	Pao	21	5.02 \pm 0.42	2.77 \pm 0.11	2.12 \pm 0.08	1.37 \pm 0.08	1.28 \pm 0.08
	Cascada	26	6.00 \pm 0.27	3.54 \pm 0.15	2.45 \pm 0.12	1.70 \pm 0.11	1.29 \pm 0.06
	Sábalo	27	5.08 \pm 0.34	2.78 \pm 0.21	2.20 \pm 0.14	1.61 \pm 0.15	1.23 \pm 0.11
	SHO 750	32	6.85 \pm 0.50	3.75 \pm 0.24	2.75 \pm 0.15	1.90 \pm 0.17	1.31 \pm 0.08
Tropical Wet	Terciopelo	0.7	5.60 \pm 0.37	3.54 \pm 0.19	2.61 \pm 0.26	1.94 \pm 0.22	1.44 \pm 0.15
	TUVA	1	3.25 \pm 0.13	2.18 \pm 0.11	1.56 \pm 0.17	0.91 \pm 0.11	0.54 \pm 0.10
	Culebra	3	5.65 \pm 0.51	3.31 \pm 0.29	2.27 \pm 0.15	1.65 \pm 0.16	1.21 \pm 0.12
	La Huerta	6.5	3.70 \pm 0.17	2.17 \pm 0.07	1.69 \pm 0.06	1.07 \pm 0.06	0.56 \pm 0.05
	Don Juan	9	6.67 \pm 0.50	4.53 \pm 0.45	3.22 \pm 0.39	2.06 \pm 0.12	1.40 \pm 0.06
	Tirimbina	18	7.03 \pm 0.36	3.61 \pm 0.24	2.91 \pm 0.10	1.94 \pm 0.11	1.17 \pm 0.06
	Piro	20	3.27 \pm 0.24	1.65 \pm 0.23	1.23 \pm 0.08	0.65 \pm 0.05	0.39 \pm 0.02
	Pumilio	25	6.92 \pm 0.29	3.86 \pm 0.13	2.57 \pm 0.09	1.65 \pm 0.06	1.20 \pm 0.08
	4 Ríos	29	5.39 \pm 0.31	3.19 \pm 0.12	2.36 \pm 0.14	1.52 \pm 0.16	1.13 \pm 0.08
	Caliente	35	5.49 \pm 0.45	3.10 \pm 0.39	1.55 \pm 0.16	0.77 \pm 0.14	0.40 \pm 0.05
	Palma Real	60	3.32 \pm 0.61	1.69 \pm 0.22	1.35 \pm 0.20	0.57 \pm 0.11	0.37 \pm 0.07

Appendix E. (Continued)

Life Zone	Site name	Age (yrs)	Depth interval (cm)				
			0-10	10-20	20-30	30-50	50-100
Premontane Rain	Volcán	0.5	9.90 \pm 0.77	6.89 \pm 0.37	4.96 \pm 1.20	3.68 \pm 0.39	2.84 \pm 0.27
	Vírgen María	10	14.57 \pm 1.37	9.71 \pm 0.79	7.32 \pm 0.75	4.63 \pm 0.49	2.81 \pm 0.42
	Alemán	15	17.53 \pm 0.70	10.50 \pm 0.27	6.14 \pm 0.48	4.12 \pm 0.41	3.10 \pm 0.36
	Cornelio	19	16.90 \pm 1.22	6.64 \pm 0.45	6.64 \pm 0.45	4.95 \pm 0.84	3.53 \pm 0.33
	Milpa	20	15.63 \pm 1.03	9.74 \pm 0.74	7.46 \pm 0.75	4.89 \pm 0.52	2.32 \pm 0.37
	Dos Ases	20	17.71 \pm 1.04	10.21 \pm 1.16	5.95 \pm 0.47	3.83 \pm 0.16	3.14 \pm 0.29
	Cambronero	30	17.30 \pm 0.81	9.47 \pm 1.09	6.03 \pm 0.75	3.58 \pm 0.46	3.55 \pm 0.31
	Hondura	35	15.95 \pm 0.50	10.66 \pm 0.27	7.86 \pm 0.12	6.19 \pm 0.32	2.96 \pm 0.26
	Vargas	40	20.46 \pm 0.90	11.33 \pm 0.52	6.63 \pm 0.56	3.47 \pm 0.16	3.52 \pm 0.22
	Kraven S.A.	50	18.33 \pm 0.73	11.16 \pm 0.67	8.53 \pm 0.78	5.52 \pm 0.46	2.55 \pm 0.39

Notes: "n.c" indicates samples were not collected; "n.a." indicates insufficient data to calculate SE.

