FOREST ECOSYSTEM RESPONSES TO EDGE EFFECTS AND SECONDARY FOREST DEVELOPMENT IN NORTHEASTERN COSTA RICA: IMPLICATIONS FOR CONSERVATION

A Dissertation
Presented in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy
with a Major in Natural Resources
in the College of Graduate Studies
University of Idaho

and with a Concentration in Tropical Forestry
in the Graduate School
Centro Agronómico Tropical de Investigación y Enseñanza

by
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January 2007

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ABSTRACT

The landscape of northeastern Costa Rica is characterized by fragmented forests interspersed with pasture and agricultural land. Knowledge of ecosystem responses to forest edge effects and the recruitment of new secondary forests is critical to regional conservation planning directed at increasing forest cover.

Forest structure was examined at 20+ year old forest-pasture edges to assess edge effects. Stem density was significantly higher at forest edges than interiors due to an increase in small diameter trees close to edges. These data show that forest edges seal with dense vegetation in the 20+ years following edge creation, suggesting that edges are robust and likely to promote high-value environmental services in these forests.

Measures of water-use efficiency (WUE) and stable carbon isotopes ($\delta^{13}C$) were used to evaluate changes in forest function at edges. No changes in foliar $\delta^{13}C$ and thus WUE were detected in *Pentaclethra macroloba*, consistent with the theory that these forests develop resilient edges. A significant depletion in the $\delta^{13}C$ of soil respired CO_2 was found at forest edges, and may be linked to changes in species composition.

Forest recruitment and carbon dynamics were examined in a chronosequence of secondary forests. Though aboveground carbon storage increased with site age, soil carbon storage did not vary. $\delta^{13}C$ data showed that soil carbon turned over within 10 years of pasture abandonment. Rapid recovery of aboveground carbon storage and soil carbon cycling highlights the conservation value of these secondary forests.

To evaluate Costa Rica's 1996 Forestry Law initiating environmental service payments (*pago por servicios ambientales*, PSA) and prohibiting deforestation, landcover data were used to compare forest change before and after 1996. A decline in natural forest loss was observed after 1996. This indicated that PSA helped to retain forest, a finding corroborated by landowner data. Increased forest connectivity over time was related to recruitment of tree plantations and secondary forests. Secondary forest carbon storage approached primary forest levels after 25-30 years, but few landowners retained natural regeneration. As a result, secondary forests will persist as minor landscape components without incentives. This case study provides evidence that PSA can be effective in retaining natural forest.

ACKNOWLEDGEMENTS

Thanks to my major professor, Katy Kavanagh, for providing me with the freedom to find my own way, as promised during one of our first conversations. Thanks also to Bryan Finegan, my co-advisor at CATIE, for his continued interest, enthusiasm, and dedication. The support and encouragement of both Katy and Bryan has been invaluable in the completion of this research. John Marshall and Paul McDaniel, as my other two committee members, were always available to discuss various questions as the need arose. Their feedback and suggestions have been an important part of this work.

Many people at CATIE were instrumental in providing logistical support and assistance in the field, both on the ground and up in the trees, including Edwin Pereira, Diego Delgado, Leonel Coto, and Gerardo Barquero. Others who assisted with fieldwork include Eduardo Zamora, Marvin Zamora, Vicente Herra, José Manuel Ulate, Aki Koyama, and Ryan Toohey. Thanks to those at FUNDECOR for their unwavering support of this research, particularly Germán Obando and Andrés Sanchún. Without their extensive knowledge of the Sarapiquí landscape, I would still be looking for field sites. I am grateful to many landowners in the Sarapiquí region who provided me access to their farms and forests.

Many people helped me to stay on top of things by handling my samples while I was busy getting my hands dirty in the field. Stacy Sesnie, Benjamin Jerabek Miller, Erika Barrientos, and Bertha Gonzalez help process and analyze agonizingly small, but important *Pentaclethra macroloba* foliage samples. Yaneth Sanchez assisted by processing many soil samples. Bob Brander, formerly of the Idaho Stable Isotopes Laboratory, was a steady and reliable presence in the lab, and I am grateful for his assistance. Kirsten Stephan and Becki Saari helped process samples for isotopic analysis when I was either too busy or too far away to do it myself. Jennifer Nalder's fast fingers helped tremendously in packing many soil and foliage samples.

Thanks to Robin Chazdon and Juan Pablo Arroyo for being generous enough to share both data and their rare 20+ year old secondary forest field sites with me. Thanks also to Paulo Olivas for providing LAI data from a study at the La Selva Biological Station. Nelson Zamora and staff at INBio assisted in identifying the many uncommon woody species we encountered in Sarapiquí's secondary forests.

I am grateful to Manuel Guariguata, Jorge Meave, and one anonymous reviewer for their insightful comments on earlier versions of Chapter 1. Steve Blecker provided a review of an earlier version of Chapter 3, after being talked into it late one night in Memphis. I gratefully acknowledge all co-authors on the integrated team paper that is Chapter 4. I would particularly like to thank Celia Harvey, Bryan Finegan, and J.D. Wulfhorst for their tremendous efforts to ensure the success of this research. This work could never have been completed without the valuable contributions of my teammates, Steve Sesnie and Wayde Morse. Efforts related to data collection described in Chapter 4 were aided by Oscar Quirós and Jhonny Méndez, both of CODEFORSA, as well as Sandra Candela, Isabel Venegas, Zayra Ramos, Hugo Brenes, and Pablo Acuna.

I'd like to extend thanks to many students with whom I've shared my tenure at the University of Idaho and CATIE. In particular, I would like to thank Steve Sesnie, Amy Pocewicz, Kirsten Stephan, Aki Koyama, Rob Pangle, and Nerea Ubierna. These individuals have provided help and support, as well as many useful discussions over the past four years. Finally, thanks to my family for their continued support of my choices to pursue research in new and exciting places.

Support for the research described in this dissertation was provided by a fellowship from the National Science Foundation's Integrative Graduate Education and Research Traineeship (IGERT) program; grant number 0014304 to the University of Idaho.

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INTRODUCTION TO THE DISSERTATION

The Sarapiquí region of Costa Rica, located in the country's northeastern Atlantic lowlands, has been the site of rapid land use change since its opening as a frontier in the 1950's (Butterfield 1994). Forests were initially cleared to make way for cattle pastures, though more recent changes have increased landscape heterogeneity as agricultural export crops such as bananas and pineapple were introduced. These land use changes have created a fragmented forest landscape, a situation that provides the opportunity to pose ecological questions about how land use change affects forests on this landscape. The research described in this dissertation was designed to address these issues.

Chapters 1 and 2 of the dissertation describe patterns of forest structural and functional changes in relation to forest edge effects. Tropical forest fragmentation has led to the development of heterogeneous landscapes with many boundaries between land use types. In the Sarapiquí region, forest-pasture edges are a common type of boundary, and one that may affect forest structure and function across the landscape. The responses of forests to edge effects vary with time since edge creation as well as across ecosystems. Reported mid-term edge effects range from severe loss of aboveground biomass and edge erosion (Ferreira and Laurance 1997, Laurance et al. 1998) to edge stabilization and sealing by vegetation (Williams-Linera 1990, Williams-Linera et al. 1998).

Chapter 1 evaluates changes in the forest structural parameters stem density, basal area, and aboveground biomass along forest edge to interior transects. This chapter also includes data derived from hemispherical photographs to examine understory light environments along forest edge to interior gradients. Chapter 2 takes a different approach to edge effects and examines forest functional changes through the use of stable carbon isotopes ($\delta^{13}C$). Specifically, $\delta^{13}C$ data were used to infer water-use efficiency in canopy and understory trees. $\delta^{13}C$ values were also measured in mineral soil and soil respired CO_2 along forest edge to interior transects to determine whether patterns in $\delta^{13}C$ in the forest canopy were evident belowground.

Chapter 3 addresses soil carbon storage and turnover in a chronosequence of secondary forests developing on abandoned pasture. The evergreen tropics store approximately one-fifth of the world's soil carbon (Jobbágy and Jackson 2000), representing a significant carbon pool. Land use change in the tropics from forest to agriculture often results in significant losses of soil carbon (Schlesinger 1997), a process that can have far-reaching global consequences. When this pattern is reversed and secondary forests recover on abandoned agricultural land, increases in soil carbon storage can occur (Rhoades et al. 2000, Feldpausch et al. 2004) and may be accompanied by carbon cycle recovery (de Camargo et al. 1999). However, this pattern has only been documented at a limited number of sites and many region- and site-specific factors (e.g. topography, soil mineralogy) influence the distribution and retention of carbon in soils (Post and Kwon 2000). As secondary forests become increasingly common in the tropics following agricultural land abandonment (Wright 2005), their potential to store and cycle carbon must be studied regionally. As such, mineral soil carbon storage as well as mineral soil and soil respired CO_2 $\delta^{13}C$ values were measured in the surface soils (0-30 cm) of sites in Sarapiquí with naturally regenerating secondary vegetation.

Chapter 4 is an interdisciplinary chapter that includes elements of land cover change, social science, and ecosystem ecology. The focus of this chapter is on the influences of Costa Rica's 1996 Forestry Law and environmental service payment program (*pago por servicios ambientales*, PSA) on forest retention and recruitment in a biological corridor. As forest loss and fragmentation increase globally, threats to biodiversity, ecosystem processes, and human welfare also rise (Millennium Ecosystem Assessment 2005). Environmental service payments to landowners have recently emerged as a mechanism to protect forests and associated resources on privately owned land (Pagiola et al. 2002). While this approach has been promoted internationally, little information exists to evaluate the efficacy of payment programs to protect and restore forests. As a case study, Costa Rica provides a prime example of a country that has incorporated environmental service payments on >500,000 ha of land with payments totaling more than US$124 million since 1996 (FONAFIFO 2006). The country's current PSA program was initiated with a 1996 Forestry Law that also provided a legal definition of forest and prohibited the clearing of forest land. PSA is available to landowners participating in forest protection and reforestation programs designed to support biodiversity conservation, carbon sequestration, watershed protection, and aesthetic values (Snider et al. 2003).

To examine the influence of PSA and the ban on forest clearing initiated by the 1996 Forestry Law, changes in forest cover within Costa Rica's San Juan – La Selva Biological Corridor were examined before and after implementation of the law. Retention of natural forest as well as recruitment of forests via tree plantations and secondary forest development were observed from classified Landsat TM images. Landowner surveys directed at both PSA participants and non-participants were used to corroborate changes observed in the landcover change analysis. Finally, aboveground and belowground carbon storage in secondary forests was examined to provide baseline data for the region, given the potential of these forests to meet PSA program objectives.

All chapters in this dissertation are formatted as manuscripts to be submitted for publication. Chapter 1 was accepted for publication at the journal Biotropica with Drs. Bryan Finegan and Kathleen Kavanagh as co-authors. Chapter 2 was submitted to the journal Oecologia with Dr. Kathleen Kavanagh as a co-author. Chapter 3 has been submitted to the journal Global Change Biology with Dr. Kathleen Kavanagh as a co-author. Chapter 4 will be submitted to the journal Landscape Ecology and is the result of a collaborative interdisciplinary effort by three doctoral students in the University of Idaho/CATIE IGERT Program, Steven Sesnie, Wayde Morse, and myself. This chapter will appear in each of our dissertations. Other co-authors on this chapter include Drs. Bryan Finegan, Celia Harvey, Steven Hollenhorst, Kathleen Kavanagh, Dietmar Stoian, and J.D. Wulfhorst.

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CHAPTER 1. RAINFOREST STRUCTURE AT FOREST - PASTURE EDGES IN NORTHEASTERN COSTA RICA

Abstract

Land use change in the Sarapiquí region of Costa Rica has resulted in a fragmented forest landscape with abrupt edges between forest and pasture. Forest responses to edge effects vary widely and can significantly affect ecosystem integrity. Our objective was to examine forest structure at 20+ yr old forest-pasture edges in Sarapiquí. Three transects with 0.095 ha plots at seven distances from forest edges were established in each of six forest patches. Stem density, basal area, and aboveground biomass in trees and palms ≥ 10 cm diameter at breast height were measured in all plots. Additionally, hemispherical photographs were taken to determine leaf area index, understory light availability, and percent canopy openness. Linear mixed-effects models showed significantly higher tree stem density at forest edges, relative to interiors, a pattern reflected by increased stem density, basal area, and aboveground biomass in small diameter trees (≤ 20 cm) growing near edges. No differences in total tree basal area, aboveground biomass, or hemispherical photograph-derived parameters were detected across the forest edge to interior gradient. The recruitment of small diameter trees following edge creation has contributed to the development of dense vegetation at the forest edge and has aided in the maintenance of similar tree basal area and aboveground biomass between edge and interior environments. These data reflect on the robustness of forest edges in Sarapiquí, a characteristic that will likely minimize future detrimental edge effects and promote a number of high-value environmental services in these forests.

Introduction

Global patterns of land use change have significantly altered forested landscapes by increasing fragmentation, a process that has been concurrent with a rise in the abundance of forest edges on the landscape. Edge zones may have positive, negative, or neutral effects on abiotic and biotic factors within a forest due to the complexity of interacting factors at these boundaries (Murcia 1995, Ries *et al.* 2004). Further, edge effects may vary with time following edge creation as newly created abiotic and biotic gradients at forest edges give rise to further edge responses.

A common response at newly created edges is increased tree mortality (Williams-Linera 1990a, Chen *et al.* 1992, Ferreira & Laurance 1997, Laurance *et al.* 1998, Harper & Macdonald 2002), a change that may lead to further structural changes and influence plant and animal distributions, abundance, and diversity (Pearman 1997, Spies 1998, Beier *et al.* 2002). Newly created edges and new treefall gaps close to the forest edge increase understory light availability and give rise to enhanced seedling and sapling growth (Fetcher *et al.* 1983, Chen *et al.* 1992, Williams-Linera 1990b, Sizer & Tanner 1999). This widely reported response to forest fragmentation is often short-lived, and longer-term structural changes are more variable. A range of mid-term edge responses have been reported in forests up to ~20 yr after edge creation, including severe aboveground biomass (AGBM) loss (Ferreira & Laurance 1997; Laurance *et al.* 1997, 1998) and increased tree density and basal area at the forest edge (Williams-Linera 1990a, Williams-Linera *et al.* 1998). These responses vary by ecosystem, climatic condition, and natural disturbance regime, so detailed regional studies of intermediate-aged forest edges will help to further clarify the mid-term effects of edges on forest structure.

Within the Sarapiquí region of Costa Rica, a unique political and social context overlies a history of deforestation, lending increased consequence to local ecological studies. Sarapiquí has experienced widespread land use change since the 1950s, and steady conversion of land from forest to pasture or agricultural use has led to annual deforestation rates of 2.8-3.6 percent over the last two decades (Butterfield 1994, Sánchez-Azofeifa *et al.* 1999). Costa Rica has worked to reduce forest loss via the 1996 Forestry Law (no. 7575) that banned deforestation and placed monetary value on forests through payments for environmental services (PES). Sarapiquí is part of a regional biological corridor and is consequently a target area for PES (García 1996, Méndez 2003). Knowledge of forest edge effects in this highly fragmented landscape will help to define the quality of forest land benefiting from the PES program.

It has been suggested that forests in Sarapiquí develop edges seal with vegetation as a response to increased light available for growth at forest edges (Forero & Finegan 2002). If this is the case, it is possible that some of the detrimental effects of forest fragmentation may be attenuated in these forests, thus helping to preserve ecosystem integrity. The goal of this study was to examine forest structure at 20+ year old forest-pasture edges in Sarapiquí, and we developed predictions consistent with the hypothesis that these edges are dominated by dense vegetation. We expected to find forest edges with higher stem density, increased frequency of small diameter trees, and greater total basal area and AGBM relative to the forest interior. We also anticipated that dense forest cover would result in edges with higher leaf area index (LAI) and lower understory light availability and canopy openness than in the forest interior.

Methods

Study region

This study was conducted in the Sarapiquí Canton, Heredia Province, Costa Rica, in an area classified as tropical wet forest by the Holdridge life zone system (Tosi 1969). Annual rainfall is approximately 4000 mm and annual temperatures average 26ºC with little monthly variation (Sanford *et al.* 1994). The forests of the Sarapiquí region are highly fragmented and the surrounding agricultural matrix is comprised primarily of pasture land and agricultural plantations (Butterfield 1994).

The upland forests of Sarapiquí are dominated by a single leguminous tree species, *Pentaclethra macroloba* (Willd.) Kuntze, that represents 32-35 percent of the total basal area in these forests (Clark & Clark 2000). The dominance of *P. macroloba* decreases with elevation and is not found at elevations > 250 m a.s.l. (Lieberman *et al.* 1996). These forests are also characterized by the presence of mid-story palms, that account for 22-25 percent of all stems > 10 cm diameter at breast height (dbh, 1.37 m) at elevations ≤ 100 m (Lieberman *et al.* 1996). In addition to *P. macroloba*, the most abundant trees in these forests are *Tetragastris panamensis* (Engl.) Kuntze, *Carapa guianensis* Aubl., and *Licania affinis* Fritsch, and the dominant palms are *Welfia regia* Mast., *Iriartea deltoidea* Ruiz & Pav., *Socratea exorrhiza* (Mart.) H. Wendl., and *Euterpe precatoria* Mart.

Site selection

Six forest sites on privately owned land with a forest-pasture border 20-30 yr old were selected for this study (Fig. 1). This age limit was chosen so that we could focus on the mid-term effects of edge creation that occur following the initial reassortment and restabilization of physical gradients at newly created edges (Matlack 1994). Individual landowners were interviewed to establish the year in which pastures were created and point data were collected with a GPS unit (GPS III, Garmin International, Kansas, USA) at each forest edge. To verify that forest edges were at least 20 yr old, analog aerial photographs acquired in 1983 (Instituto Geográfico Nacional, San José, Costa Rica) were visually compared to the GPS data overlaid on a Landsat TM image acquired in 2001.

We studied forest edges adjacent to pasture rather than those adjacent to other common land uses in the area (*e.g.* tree plantations, agriculture) because the strength of edge effects is often greatest between land uses with abrupt changes in vegetation density and structure (Ries *et al.* 2004). It should be noted that some structural heterogeneity existed in pastures adjoining forest patches, as all had remnant trees and some also contained live fences. Study sites were located between 50 and 200 m a.s.l. (Table 1) on gently rolling terrain. Sites 1 and 3 were located on acidic, highly weathered Ultisols derived from volcanic parent materials and all other sites were situated on Inceptisols derived from Quaternary alluvial deposits (ITCR 2004).

All study sites were located on land adjacent to other forested tracts; therefore the forest area sampled at each site (Table 1) represents only the forest land area belonging to an individual landowner. No attempt was made to quantify the extent of the forest area in which study sites were imbedded because in some cases the adjoining forest was part of an extensive national park (Fig. 1). All sites were either unmanaged primary forest (Sites 3 and 6) or had been selectively harvested for timber in the past under approved sustainable forest management plans (Table 1).

Field sampling

Within study sites, areas with streams running parallel or perpendicular to the forest edge were excluded as sampling sites to reduce variation introduced by riparian vegetation. A set of three transects perpendicular to the forest edge were randomly situated at each site. Within transects, plots were established at distances of 0, 25, 50, 100, 150, 200, and 300 m from the forest edge. The numbers used to describe the plots represent the plot boundary closest to the forest edge. Each plot consisted of three adjacent circular subplots laid out parallel to the forest edge. The radius of each circular subplot was 10 m, so the total plot area sampled at each distance was 942.5 m^2. In most cases, the distance between transects (*i.e.*, the distance from the end of one plot boundary to the beginning of the next plot boundary in the adjacent transect) was at least 100 m. However, short forest-pasture edges led us to reduce this distance to 22 m at Site 2 and 50 m at Site 6.

In each plot the dbh of all trees and palms ≥ 10 cm dbh was measured with a fabric diameter tape. Diameter measurements were made above stilt roots or buttresses when present, and when physical measurements were not possible tree diameters were estimated visually. These measurements were used to calculate the stem density (number of stems/ha) and basal area for both trees and palms. These data were also used to estimate tree AGBM using Brown and Iverson’s (1992) equation for wet tropical forests,

$$Y = 21.297 - 6.953(D) + 0.740(D^2)$$

where Y is biomass per tree in kg and D is dbh in cm. Biomass estimates derived from this equation represent the biomass of the bole as well as that of all leaves, twigs, branches, and bark. Estimates of palm AGBM were not made because accurate prediction equations do not exist for the palm species common in Sarapiquí. Tree data were divided into five diameter classes (10-15, 15.1-20, 20.1-30, 30.1-60, ≥ 60.1 cm dbh) to examine the contribution of each class to total tree stem density, basal area, and AGBM.

Hemispherical photographs were taken with a digital camera fitted with a fisheye lens (Coolpix 4500, Fisheye Converter FC-E8, Nikon Corporation, Tokyo, Japan) at each plot center. Photographs were taken with the top of the camera oriented toward north under uniformly overcast sky conditions at a height of 1 m above the forest floor. Camera aperture and shutter speed were allowed to vary with lighting conditions to obtain the most balanced image possible. Hemispherical photographs were analyzed by a single operator using HemiView Canopy Analysis Software (version 2.1, Delta-T Devices Ltd., Cambridge, UK).

Variables derived from image analysis included LAI, global site factor (GSF), and canopy openness. LAI is defined as half the total leaf area per unit ground area, but in this study we effectively measured plant area index (PAI) because hemispherical photographs include woody elements in the canopy (*e.g.* tree boles, branches) (Weiss *et al.* 2004). For the sake of consistency, we use the term LAI in lieu of PAI because most values of hemispherical photograph-derived LAI in the literature represent PAI. GSF is a term that combines direct and diffuse light in the understory and expresses it relative to total light availability above-canopy. Weighting factors for direct and diffuse light in the understory were used in the calculation of GSF (Rich *et al.* 1993). Canopy openness was calculated as a percentage from the visible sky term generated from the analysis of each photograph.

Data analysis

The design of this study, in which three identical transects were nested within each study site, lent itself to the use of linear mixed-effects models (Pinheiro & Bates 2000). These models contain both fixed and random effects and, in circumstances like those in the present study, are analogous to a blocked design. Fixed effects are parameters associated with a population and the estimates of these parameters are of primary importance in mixed-effects models. In contrast, estimates of random effects are not centrally important to questions about a population, as they represent grouped covariates in the data. In this study, the fixed effect was 'distance to forest edge', specified as a continuous variable, and the factors 'transect' nested within 'site' were specified as the random effects in all models.

The mixed-effects model configuration described above was used in analyses of the following variables: palm stem density and basal area, tree stem density, basal area, and AGBM for all diameter classes pooled and for each of the five diameter classes described above, LAI, GSF, and canopy openness. Data transformations suggested by Box-Cox tests (Box & Cox 1964) were used as needed to normalize data prior to analysis. Specifically, a square root transform was used for all palm data, as well as for all tree data from the 10-15, 20.1-30, and 30.1-60 cm dbh classes. A log transform was used to normalize tree basal area and AGBM data and a reciprocal square transform was used for LAI data.

Analysis of variance (ANOVA) was used to examine each of these variables in relation to the fixed effect, distance to the forest edge. Significant differences detected along forest edge to interior gradients with ANOVA were not further evaluated with multiple comparisons because the fixed effect was analyzed as a continuous rather than a categorical variable. All data processing, model fitting, and analyses were performed using the open-source statistical language R (version 2.0.1, R Development Core Team 2004).

Results

Forest structural parameters

Among trees, stem density was significantly higher (ANOVA, $F = 8.495$, df = 104, $P = 0.0044$) in plots close to the forest edge and ranged from a maximum of 549 ± 27 stems/ha (throughout the text, ± values represent one SE) at 0 m to a minimum of 415 ± 20 stems/ha at 300 m (Fig. 2a). The opposite pattern was observed for palms, with significantly higher stem density (ANOVA, $F = 33.9753$, df = 104, $P < 0.0001$) observed in forest interior plots, relative to edge plots (range: 42 ± 10 stems/ha at 0m to 94 ± 13 stems/ha at 300 m; Fig. 2a). Palms also exhibited significantly greater basal area (ANOVA, $F = 25.5230$, df = 104, $P < 0.0001$) in the forest interior than at the edge (range: 0.9 ± 0.2 m^2/ha at 0m to 1.6 ± 0.2 m^2/ha at 300 m; Fig. 2b). Neither basal area nor AGBM varied significantly for trees along the forest edge to interior gradient (Fig. 2b and c). Among trees, mean basal area was 24.6 ± 0.6 m^2/ha, while mean AGBM was 170.3 ± 4.5 Mg/ha. For all stems ≥ 10 cm dbh, palms occupied between 7 and 18 percent of the total stem density and between 3 and 6 percent of the total basal area.

Tree data were divided into five diameter classes to explore the contribution of different diameter classes to total tree stem density, basal area, and AGBM. Within the class of stems from 10-15 cm dbh, a trend toward higher stem density at the forest edge was observed (Fig. 3a), but was marginally non-significant (ANOVA, $F = 3.6633$, df = 104, $P = 0.0584$). However, significantly greater basal area (ANOVA, $F = 4.7347$, df = 104, $P = 0.0318$) and AGBM (ANOVA, $F = 5.1587$, df = 104, $P = 0.0252$) were found for this diameter class in plots closest to the forest edge (Fig. 3b and c). Similarly, in the 15.1-20 cm dbh class, significantly greater stem density (ANOVA, $F = 6.1882$, df = 104, $P = 0.0144$), basal area (ANOVA, $F = 5.9416$, df = 104, $P = 0.0165$), and AGBM (ANOVA, F = 5.8183, df = 104, $P = 0.0176$) were observed at forest edges (Fig. 3a–c). No significant differences in these forest structural parameters were found in the remaining two diameter classes, 20.1-30 and 30.1-60 cm dbh (Fig. 3a–c). Statistical analyses could not be performed for stems ≥ 60.1 cm dbh because these individuals were rare given the total land area sampled. Thirty-one percent of plots contained no trees in this diameter class and 46 percent of plots contained only one tree ≥ 60.1 cm dbh.

Leaf area index and understory light availability

LAI did not differ along the forest edge to interior gradient (Table 3). Mean LAI across all sites and distance classes was 3.41 ± 0.08 m^2/m^2. Similarly, GSF and canopy openness were invariant along the edge to interior gradient (Table 2).

Discussion

Forest structural parameters

Consistent with our overarching hypothesis, forests in the Sarapiquí region of Costa Rica developed a dense wall of vegetation at forest edges in the 20+ yr following edge creation.

Specifically, we observed elevated tree stem density at forest edges, and this pattern was reflected by higher stem density, basal area, and AGBM for trees in small diameter classes growing close to forest edges. This indicates that the germination and growth of small diameter trees following edge creation was instrumental in sealing forest edges with vegetation. The presence of dense vegetation at forest edges has likely stabilized these forests and contributed to the structural similarity between forest edge and interior environments observed for both tree basal area and AGBM. The decline in palm stem density and basal area detected at forest edges may be the result of human harvesting pressures, given the gradual increase in both of these variables with increased distance from the edge.

Measures of tree stem density, basal area, and AGBM compare favorably with those made in undisturbed primary forests at the nearby La Selva Biological Station (10° 26' N, 83° 59' W, 35-137 m a.s.l., see Fig. 1). Mean tree stem density, basal area and AGBM data fell within the range of values reported at La Selva, though the La Selva study included palms in measures of these variables (Clark & Clark 2000). In relation to other studies of edge effects in the Neotropics, these results are most consistent with findings in Panamanian premontane wet forest and low-elevation tropical forest in Mexico (Williams-Linera 1990a, Williams-Linera *et al.* 1998), indicating that similar processes of edge development may exist across these ecosystems.

Shifts in species composition favoring early successional species at forest edges have been reported in Sarapiquí and related to an increase in small diameter trees at forest edges (Forero and Finegan 2002). A similar increase in early successional species at edges has also been reported in the experimentally fragmented forests of the Biological Dynamics of Forest Fragments Project (BDFFP) in the Brazilian Amazon (Laurance *et al.* 2006). However, the long-term implications for forest structural responses to edge effects are likely to differ between these two systems.

The observed increase in pioneer species abundance at edges in the BDFFP has been related to chronic wind disturbance and AGBM loss at edges (Kapos 1989, Ferreira & Laurance 1997, Laurance *et al.* 1997). These changes are expected to trigger additional biotic and abiotic edge effects, leading to the degradation of these forest fragments over time (Laurance *et al.* 2002). Although the present study does not focus on changes in edge structure with time, the presence of dense vegetation at the forest edge and the similarity of basal area and AGBM in edge and interior locations indicate that edges in Sarapiquí are not subject to chronic disturbances or significant AGBM loss. It is likely that many edge effects, including microclimatic changes and those influencing plant and animal distribution and abundance, will be attenuated in these forests due to the presence of dense vegetation at forest edges (Didham & Lawton 1999). Future investigation will be needed to further clarify the role of successional vegetation in stabilizing forest edges in Sarapiquí over the long-term.

In general, drawing conclusions about long-term edge effects on forest structure is difficult in most ecosystems because old forest fragments are rare. Most studies addressing long-term edge effects have focused on gallery forests in the savanna ecosystems of Central America thought to have been established at the beginning of the Holocene (MacDougall & Kellman 1992, Meave & Kellman 1994, Kellman *et al.* 1996). Though isolated, these forest fragments have persisted through time and are maintained by dense vegetation at the forest edge (Kellman *et al.* 1996). This feature has been effective in stabilizing these extremely old forest fragments, suggesting that Sarapiquí's fragmented forests may also be protected by this shared attribute.

Leaf area index and understory light availability

LAI, GSF, and canopy openness did not vary along the forest edge to interior gradient. Although higher LAI was predicted at the forest edge relative to the interior, a lack of significant variation along this gradient reflects the findings discussed above. Increased understory light availability has been reported in other Neotropical forests with edges dominated by dense vegetation, but this increase was always confined to the immediate edge (~5-10 m from the edge) (Williams-Linera 1990a, MacDougall & Kellman 1992). In the present study, hemispherical photographs in edge plots were taken at distance of 10 m from the edge, and may not accurately represent the understory light environment at points closer to the edge. Overall, our data indicate that understory light availability is not likely to differentially influence future seedling development and sapling recruitment at the edge relative to the forest interior.

Recent research indicates that LAI is typically underestimated by digital hemispherical photographs relative to film-derived estimates of LAI, in part because GSF and canopy openness are overestimated in digital photographs (Englund *et al.* 2000, Frazer *et al.* 2001).

Additionally, destructive sampling of canopy foliage for LAI determination has shown that digital hemispherical photography considerably underestimates LAI in the forests of Sarapiquí (P. Olivas, personal communication). Although the LAI values presented in this paper may not reflect true LAI, it should be recognized that as a relative measure LAI was invariant across the forest edge to interior gradient.

Conservation implications

The study region lies within the boundaries of the San Juan – La Selva portion of the Mesoamerican Biological Corridor, a regional corridor designed to connect protected forests in Costa Rica's central mountains to those in southern Nicaragua. Corridor objectives include protecting habitat for the endangered Great Green Macaw (*Ara ambiguus*), as well as decreasing forest fragmentation, promoting biodiversity conservation, and contributing to sustainable resource use (Chassot & Monge 2002). Because the Corridor has been a target area for Costa Rica's PES program (García 1996, Méndez 2003), a relatively high ecological value has been placed on forests of the region.

Forest edge structure is of central importance in attenuating abiotic and biotic edge effects in fragmented forest patches (Didham & Lawton 1999). As such, the structural integrity of forest edges in Sarapiquí will be beneficial in maintaining forest productivity as well as processes such as water and nutrient cycling (Landsberg & Gower 1997, Spies 1998). Further, many organisms dependent upon remaining forest patches for survival will benefit from the presence of robust edges, as forest structural parameters are often linked to the maintenance of biodiversity (Bawa & Seidler 1998, Brokaw & Lent 1999). Given the concentration of conservation efforts directed at the Sarapiquí region, data from the present study confirm that these forests are valuable and worthy of this high level of attention.

Acknowledgements

This research was supported in part by NSF-IGERT grant no. 0114304. Thanks to CATIE and FUNDECOR, particularly Germán Obando and Andrés Sanchún, for project support. Edwin Pereira, Steven Sesnie, and Nerea Ubierna contributed logistical support important to this research, Paulo Olivas provided data, and Eduardo Zamora assisted with fieldwork. We are indebted to many landowners in the Sarapiquí region, without whom this research would not have been possible. Thanks also to Manuel Guariguata, Jorge Meave, and one anonymous reviewer for their insightful comments on earlier versions of this manuscript.

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Table 1. Site characteristics for the six study sites. Name, elevation, size of sampled forest area, site history characteristics (SH = selectively harvested for timber, UH = unharvested) followed by date of last harvest, and summary statistics for tree stem density, basal area, and aboveground biomass (AGBM) (mean ± one SE) in each study site. Summary statistics were calculated based on measurements of all trees ≥ 10 cm dbh.

Site	Elevation (m a.s.l.)	Size (ha)	Site History	Stem Density (# stems/ha)	Basal Area (m^2/ha)	AGBM (Mg/ha)
1	58	375	SH, 1991	427 ± 14	21.5 ± 0.8	148.1 ± 6.2
2	62	120	SH, 2000	461 ± 26	25.4 ± 1.2	177.2 ± 9.0
3	116	196	UH	411 ± 22	25.4 ± 1.4	180.8 ± 10.9
4	66	111	SH, 1995	486 ± 25	27.6 ± 1.4	192.8 ± 10.1
5	176	139	SH, 2003	522 ± 28	23.4 ± 1.7	155.2 ± 12.3
6	200	80	UH	488 ± 33	24.2 ± 1.8	164.8 ± 13.7

Table 2. Mean ± one SE of leaf area index (LAI), global site factor (GSF), and canopy openness relative to distance to the forest edge. No significant differences were observed along the forest edge to interior gradient.

Distance Class (m)	LAI (m^2/m^2)	GSF (%)	Canopy Openness (%)
0	3.33 ± 0.21	9.2 ± 0.8	5.9 ± 0.5
25	3.50 ± 0.28	9.8 ± 0.9	6.0 ± 0.6
50	3.42 ± 0.21	9.7 ± 0.8	5.9 ± 0.5
100	3.25 ± 0.16	10.1 ± 0.6	6.2 ± 0.4
150	3.20 ± 0.15	8.4 ± 0.7	5.5 ± 0.5
200	3.91 ± 0.31	10.4 ± 0.6	6.0 ± 0.4
300	3.29 ± 0.15	8.9 ± 0.6	5.6 ± 0.4

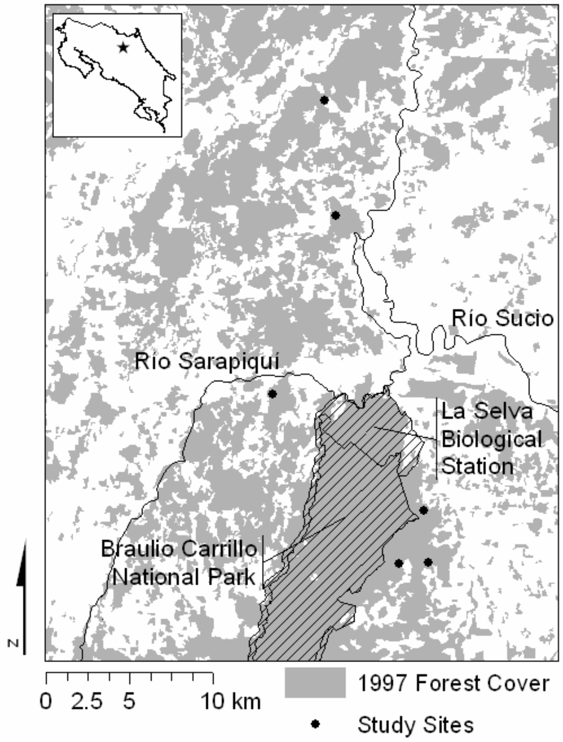

Figure 1. Map of the study area within Costa Rica. Inlay of Costa Rica indicates the location of the Sarapiquí region with a star. The detailed map shows the location of all study sites as black dots. Grey shaded areas represent forest cover in 1997 and areas covered by hatching are national parks and protected areas (ITCR 2004).

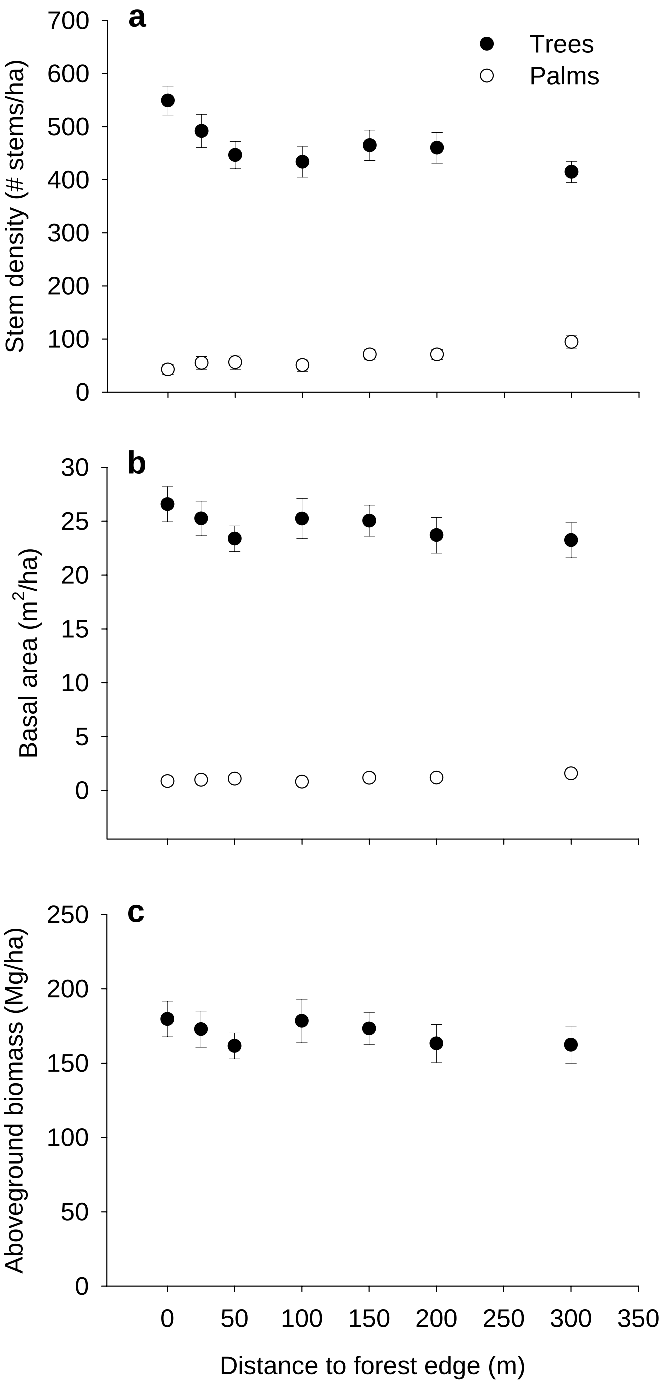

Figure 2. Mean ± one SE of (a) stem density, (b) basal area, and (c) aboveground biomass (AGBM) for trees and palms in relation to the distance of each plot from the forest edge. AGBM estimates for palms were not made because accurate prediction equations do not exist. Significant differences in tree and palm stem density ($P = 0.0044$, $P < 0.0001$, respectively) and palm basal area ($P < 0.0001$) were detected among distance classes.

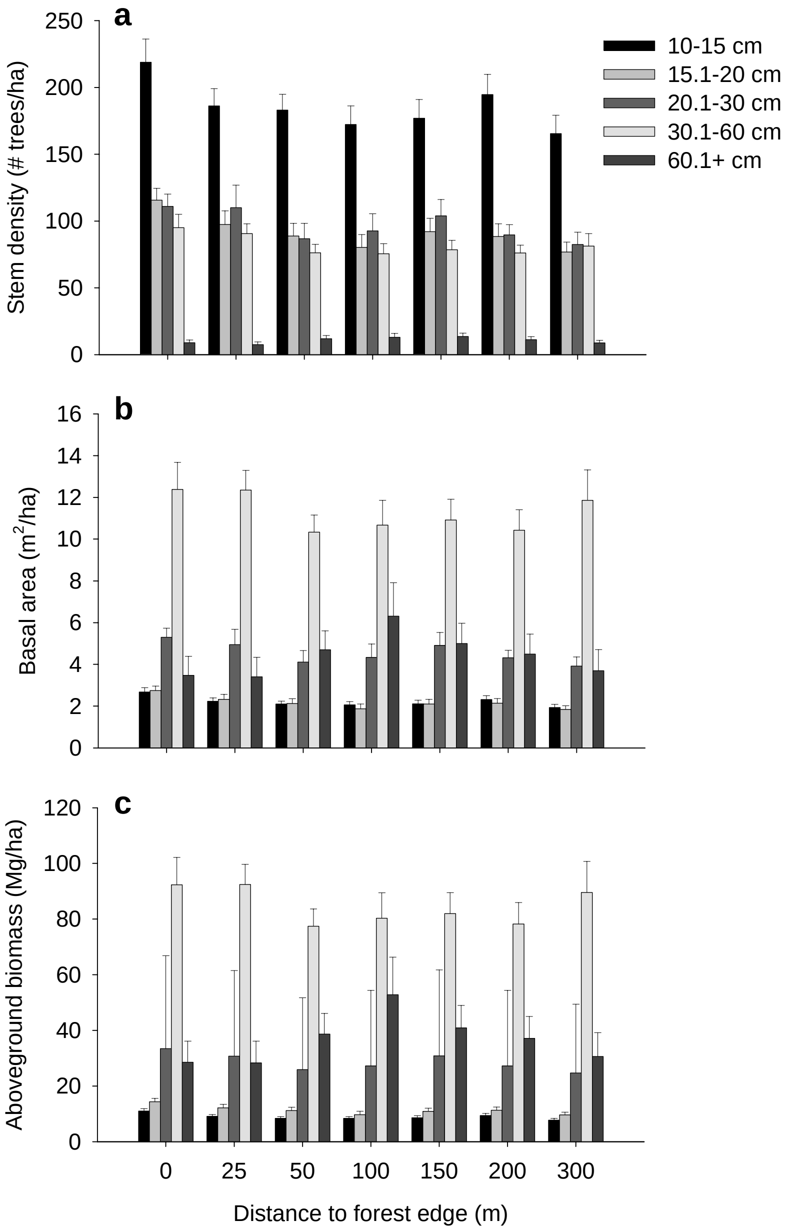

Figure 3. Mean ± one SE of (a) stem density, (b) basal area, and (c) aboveground biomass (AGBM) for trees in five diameter classes in relation to the distance of each plot from the forest edge. Significant differences along the forest edge to interior gradient were found for basal area (*P* = 0.0318) and AGBM (*P* = 0.0252) in the 10-15 cm diameter class and for stem density (*P* = 0.0144), basal area (*P* = 0.0165), and AGBM (*P* = 0.0176) in the 15.1-20 cm diameter class. Statistical analyses were not performed for the 60.1+ cm diameter class because of the small number of individuals in this category.

CHAPTER 2. WATER-USE EFFICIENCY AND δ^{13}C AS INDICATORS OF FOREST EDGE EFFECTS IN NORTHEASTERN COSTA RICA

Abstract

Functional responses of forests to edges created by disturbance are rarely studied, though stable carbon isotope ($\delta^{13}C$) data can be effectively used in this capacity. Specifically, changes in leaf level $\delta^{13}C$ ($\delta^{13}C_{leaf}$) can reflect changes in canopy processes such as photosynthesis and transpiration, the components of water-use efficiency (WUE). Environmental conditions commonly observed at forest edges can decrease stomatal conductance, thereby increasing $\delta^{13}C_{leaf}$ and WUE. We tested the hypothesis that $\delta^{13}C_{leaf}$ would be enriched in ^{13}C and WUE would be higher in trees growing close to forest edges. We expected that these shifts would also be detectable belowground in the $\delta^{13}C$ values of soil organic matter ($\delta^{13}C_{soil}$) and soil respired CO_2 ($\delta^{13}C_{R\text{-}soil}$). To evaluate these hypotheses, a set of three transects perpendicular to the forest edge were established in each of three tropical rainforest fragments in northeastern Costa Rica. Canopy and understory foliage from *Pentaclethra macroloba* trees, soil respired CO_2, and mineral soil samples were collected between 0 and 300 m from the forest edge. $\delta^{13}C_{leaf}$, $\delta^{13}C_{soil}$, and $\delta^{13}C_{R\text{-}soil}$ were determined with mass spectroscopy, and foliar data were used to estimate WUE. Data were analyzed using linear mixed-effects models. Contrary to our predictions, $\delta^{13}C_{leaf}$ and WUE did not differ along the edge to interior gradient, and this lack of variation was also apparent in $\delta^{13}C_{soil}$. However, $\delta^{13}C_{R\text{-}soil}$ was significantly more depleted within 50 m of forest edges relative to the forest interior ($p = 0.0347$). This change may be related to a shift in species composition at the edge, but further research is needed to verify this hypothesis. The predominant lack of functional responses to the presence of edges in northeastern Costa Rica indicates that trees at these forests edges are robust and minimally influenced by edge effects.

Introduction

The structure, species composition, and dynamics of forest ecosystems are often studied to describe forest responses to edge effects. However, few studies have focused on forest functional responses to edges as a means of exploring why these variables may change at forest edges. In shifting edge effects research toward forest functional responses, stable carbon isotope analysis can be used to address questions about water-use efficiency (WUE) in forest trees (Farquhar and Richards 1984). WUE, defined as the ratio of CO_2 assimilation to transpiration, describes the relationship between carbon gain and water loss at the leaf level. Foliar stable carbon isotope values ($\delta^{13}C_{leaf}$) can be used to estimate WUE.

WUE can be used as an indicator of a tree's functional response to environmental gradients (e.g. Ehleringer et al. 1986), such as those present at forest edges. Modified growing conditions at edges, including high light, temperature, and vapor pressure deficit (VPD), are common across ecosystems (Kapos 1989; Chen et al. 1995; Williams-Linera et al. 1998; Newmark 2001) and may influence tree growth and survival (Laurance et al. 2002). Specifically, these conditions can lead to more stomatal closure in response to factors such as increased evaporative demand at the leaf level or decreased soil moisture. Reductions in stomatal conductance decrease water loss and lead to an increase in $\delta^{13}C_{leaf}$.

In C_3 plants, discrimination against the heavier carbon isotope, as $^{13}CO_2$, occurs during CO_2 assimilation by a leaf. Diffusive fractionation and a strong biochemical fractionation by ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) against $^{13}CO_2$ molecules constitute the strongest sources of discrimination during CO_2 assimilation (Farquhar et al. 1989; Farquhar and Lloyd 1993). A third significant source of discrimination has been documented as a process concurrent with CO_2 transfer conductance from the substomatal cavity of a leaf to the sites of carboxylation in the mesophyll (Lauteri et al. 1997; Warren et al. 2003; Warren and Adams 2006). Net discrimination against $^{13}CO_2$ molecules during photosynthesis decreases the likelihood that $^{13}CO_2$ will be assimilated when the intercellular CO_2 concentration of a leaf (c_i) is high and $^{12}CO_2$ molecules are readily available. However, as c_i declines following a reduction in stomatal conductance, $^{13}CO_2$ is necessarily assimilated with greater frequency. As such, foliage with a $\delta^{13}C_{leaf}$ enriched in ^{13}C is linked to low discrimination, low c_i, and high WUE (Farquhar and Richards 1984).

While variation in stomatal conductance is partially responsible for determining $\delta^{13}C_{leaf}$, carbon available at the time of leaf formation, environmental conditions, and leaf-level photosynthetic capacity are also influential. Once created, structural carbon compounds within a leaf are relatively stable for the duration of the leaf's life-span. Therefore, carbon available at the time of leaf formation and the prevailing growing environment (e.g. low vs. high moisture conditions) under which that carbon was fixed can influence the $\delta^{13}C_{leaf}$ (Leffler and Evans 2001; Keel et al. 2006). In terms of photosynthesis, leaves with high photosynthetic capacity such as those growing in forest canopies under full sun tend to maintain a low c_i (Hanba et al. 1997; Duursma and Marshall 2006), a parameter influential in determining $\delta^{13}C_{leaf}$ (Farquhar and Richards 1984). Thus, for a given stomatal aperture, leaves with higher photosynthetic capacity will assimilate more $^{13}CO_2$ relative to leaves with lower photosynthetic capacity. Photosynthetic capacity can be examined indirectly via leaf nitrogen content and specific leaf area (SLA), as both parameters are well correlated with maximum net photosynthesis (Field and Mooney 1986; Reich et al. 1992; Reich et al. 1997).

The components of WUE, photosynthesis and transpiration, are canopy processes that have downstream effects on plant $\delta^{13}C$ values. Specifically, as the products of photosynthesis are translocated within a plant, some become substrates for root and rhizosphere respiration. $\delta^{13}C$ values of soil respired CO_2 ($\delta^{13}C_{R\text{-}soil}$) represent a mixed signal, derived not only from sources that may rely on current photosynthate, but also from heterotrophic respiration in which soil organic matter serves as the primary respiratory substrate. Despite the variation in inputs to soil respired CO_2, climatic and environmental changes influencing the $\delta^{13}C$ of carbon fixed in the canopy is detectable in $\delta^{13}C_{R\text{-}soil}$ one to six days following initial carbon fixation (Ekblad and Högberg 2001; Ekblad et al. 2005). These data indicate that both short-term climatic changes, such as seasonal increases in VPD, and long-term changes, such as those resulting from forest edge creation, will produce $\delta^{13}C$ signals evident both above- and belowground.

We chose to examine $\delta^{13}C$ values in the ecosystem components described above: foliage, soil respired CO_2, and soil organic matter. Our goal was to determine forest functional responses to the presence of an edge in the Sarapiquí region of Costa Rica. Forests in this area of Costa Rica's Atlantic lowlands are primarily classified as tropical wet forest by the Holdridge life zone system (Tosi 1969) and exhibit little annual variation in either rainfall or temperature (Sanford et al. 1994). A shade-tolerant, leguminous tree species, *Pentaclethra macroloba* (Willd.) Kuntze, occupies between 32 and 35% of the basal area in these high-diversity forests (Clark and Clark 2000). *P. macroloba* is found frequently in both the canopy and understory and was selected as a focal species for this study.

It has been suggested that *P. macroloba* originated as a swamp species that eventually colonized upland areas with high rainfall (Hartshorn 1972). This theory is complemented by physiological measurements that point toward a degree of water stress sensitivity in this species (Oberbauer et al. 1987). Specifically, *P. macroloba* has been shown to exhibit reduced stomatal conductance following extended exposure to full sun conditions in both field and laboratory settings (Oberbauer 1983; Oberbauer et al. 1987). Because high light conditions can increase both temperature and VPD, it is probable that *P. macroloba*'s stomatal sensitivity under high light is linked to one or both of these factors. Therefore it is likely that signs of water-related stress on trees growing near forest edges will be apparent in *P. macroloba*.

We examined two primary hypotheses. First, $\delta^{13}C_{leaf}$ will be more enriched and WUE will be higher in canopy and understory trees growing close to the forest edge, relative to those in the forest interior. Second, patterns in $\delta^{13}C_{leaf}$ detected in canopy trees will also be apparent in the mineral soil $\delta^{13}C$ value ($\delta^{13}C_{soil}$) and $\delta^{13}C_{R\text{-}soil}$. We also examined differences in canopy and understory $\delta^{13}C_{leaf}$ relative to leaf mass per unit area (LMA, the reciprocal of SLA) and nitrogen content, with the expectation that canopy $\delta^{13}C_{leaf}$ will reflect high photosynthetic capacity.

Methods

Site description

This study was conducted in the Sarapiquí region of northeastern Costa Rica. Rainfall averages approximately 4000 mm annually with a mean annual temperature of 26°C (Sanford et al. 1994). The region is characterized by fragmented forests within an agricultural matrix comprised of active pastures and crop land (Butterfield 1994).

Three sites with 20 to 30 year old forest-pasture borders were selected for this study, and all sites were located between 50 and 120 m a.s.l. on gently rolling terrain. Two sites, Rojomaca and Selva Verde, were located on highly weathered, acidic Ultisols derived from volcanic parent material while the third site, Tosi, was located on an Inceptisol derived from Quaternary alluvial deposits (ITCR 2004). Rojomaca and Tosi had been selectively harvested within 15 years of the present study, but no harvesting is known to have occurred at Selva Verde.

Foliar sampling

At each site, we established three transects perpendicular to the forest edge. Transects were randomly located and spaced 22 to 100 m apart, depending on the length of the forest-pasture edge at each site. Samples were collected in 0.1 ha plots located at distances of 0, 25, 50, 100, 200, and 300 m from the forest edge. Each plot extended 20 m into the forest, parallel to the established transects. Two canopy and two understory *P. macroloba* trees were sampled in each plot. If suitable trees could not be located within the plot, trees immediately adjacent to the plot were substituted.

A tree-climber cut one small branch from the upper third of each *P. macroloba* tree (diameter at breast height (dbh, 1.37 m) range: 19.1-82.0 cm) sampled in the forest canopy. All leaves on these branches were in full sun and came from heights of 25 to 35 m above the forest floor. From each branch, we collected 10 fully expanded leaves and avoided sampling leaves with significant epiphytic growth. A similar procedure was used to collect foliage from shaded understory *P. macroloba* trees (dbh range: 1.5-34.5 cm) at heights of 3 to 5 m above the forest floor. As foliar samples were collected, temperature and relative humidity measurements were made in the canopy and understory with a hand-held weather meter (Kestrel 4000, Nielsen-Kellerman Company, Boothwyn, PA). These data were pooled by site and plot distance and were used to calculate canopy and understory VPD.

A subset of the sampled trees, consisting of one canopy and one understory tree per plot, was selected for measurements of LMA. These measurements were not made for all trees because of the difficulty associated with processing foliage from *P. macroloba*, a species with bipinnately compound leaves and very small sub-leaflets. LMA was determined separately for three leaves per tree by selecting five leaflets per leaf for analysis. Sub-leaflets were separated from the rachis of each leaflet, scanned, dried at 70°C for 48 hours, and weighed to the nearest mg. The leaf area of scanned sub-leaflets was determined using Image-J image analysis software (v. 1.34s, National Institutes of Health, Bethesda, Maryland).

To determine $\delta^{13}C_{leaf}$ and nitrogen content (N_{mass}), 10 leaflets per sample tree were randomly selected for analysis. Sub-leaflets were removed from the leaflet rachis, dried at 70°C for 48 hours, and ground into a fine powder. $\delta^{13}C_{leaf}$ and N_{mass} were determined at the Idaho Stable Isotopes Laboratory (ISIL) using CE Instruments' NC2500 elemental analyzer coupled with the Finnigan MAT Delta-plus isotope ratio mass spectrometer (Thermo Electron Corporation, Bremen, Germany). Stable carbon isotope data are expressed in standard delta notation as,

$$\delta^{13}C = ((R_{sample}/R_{standard}) -1) \times 1000$$

where R_{sample} is the ratio of ^{13}C to ^{12}C in the sample of interest and $R_{standard}$ is the ratio of ^{13}C to ^{12}C in a standard (PDB). Twenty-two randomly selected foliar samples (10% of all samples) were analyzed in duplicate and analyses yielded a mean difference for $\delta^{13}C_{leaf}$ of 0.25‰. The nitrogen content of each leaf, expressed as a fraction, was multiplied by LMA to calculate the quantity of nitrogen per unit leaf area (N_{area}).

Within-leaf $\delta^{13}C$ variability was examined in a small subset of leaves (n = 8). For this analysis, leaflets were selected from the upper, middle, and lower third of leaves from five canopy and three understory trees. Leaflets from the middle third of these leaves were also divided into upper and lower sub-leaflets to examine within-leaflet variation in $\delta^{13}C$. Foliage was processed and analyzed as described above.

Mineral soil and soil respired CO_2 sampling

Within each plot, three mineral soil samples from 0-10 cm depth were homogenized to form a single sample. All leaf litter was removed from the soil surface prior to sampling. Soils were air-dried to constant mass, sieved through a 2 mm mesh, and a subsample was homogenized for $\delta^{13}C$ analysis. The mean difference in $\delta^{13}C_{soil}$ for six duplicate soil samples (11% of all samples) was 0.31‰.

Soil CO_2 was also collected in each plot from chambers fitted with rubber septa on the soil surface. Each chamber was inverted over a gently excavated circle in the soil, and all living plant material was removed from the area beneath the chamber. Soil from outside the study area was used to seal the edges of the chamber, and chambers were allowed to equilibrate with soil CO_2 for at least four days before an air sample was collected. Soil CO_2 samples were drawn from the chamber with a syringe and injected into evacuated 12 ml septum-capped Exetainers® (Labco Ltd., High Wycombe, UK). Samples were shipped to the ISIL and analyzed 8 to 13 days after collection. The $\delta^{13}C$ value of air samples was determined using Finnigan MAT's GasBench II coupled with the Finnigan MAT Delta-plus-XP IRMS. $\delta^{13}C$ values of soil CO_2 samples were corrected by -4.4‰ to account for the difference in diffusion rates between $^{12}CO_2$ and $^{13}CO_2$ in the soil pore space (Cerling et al. 1991). This corrected value is hereafter referred to as the $\delta^{13}C$ value of soil respired CO_2, $\delta^{13}C_{R\text{-}soil}$.

WUE estimation

Instantaneous WUE was estimated from $\delta^{13}C_{leaf}$ as follows. First, discrimination (Δ) was estimated as,

$$\Delta = (\delta^{13}C_a - \delta^{13}C_p) / (1 + \delta^{13}C_p / 1000)$$

where $\delta^{13}C_p$ is the $\delta^{13}C$ value of bulk foliar tissue or $\delta^{13}C_{leaf}$ and $\delta^{13}C_a$ is the atmospheric CO_2 $\delta^{13}C$, estimated at -8‰, the mean tropospheric value. $\delta^{13}C_a$ was assumed not to vary above a height of 1 m in the forest (Buchmann et al. 2002). Next, c_i was estimated as,

$$c_i = c_a (\Delta - a) / (b - a)$$

where c_a is atmospheric CO_2 concentration (380 ppm), a is the diffusional fractionation against $^{13}CO_2$ (4.4‰), and b is the net fractionation against $^{13}CO_2$ resulting from carboxylation by Rubisco (estimated at 28‰). Instantaneous WUE, defined as the ratio of carbon assimilation to transpiration (A/E), was estimated as,

$$A/E = (c_a - c_i) / (1.6\ \upsilon)$$

where υ is the vapor pressure difference between the leaf and atmosphere. VPD was used as a surrogate for υ, assuming that the bipinnately compound leaves of *P. macroloba* were well coupled to the atmosphere.

Statistical analyses

The statistical language R (version 2.0.1, R Development Core Team 2004) was used for all data processing and analyses. One-way analysis of variance (ANOVA) was used to test for differences in $\delta^{13}C$ in leaflets and sub-leaflets from varying leaf positions. LMA, N_{mass}, N_{area}, $\delta^{13}C_{leaf}$, WUE, $\delta^{13}C_{soil}$, and $\delta^{13}C_{R\text{-}soil}$ data were analyzed with linear mixed-effects models (Pinheiro and Bates 2000). ‘Distance to forest edge’ was analyzed as a continuous variable as each model’s fixed effect. Random effects for all models were ‘transect’ nested within ‘fragment’. Prior to analysis, WUE data were log transformed and the LMA data for understory foliage were reciprocal transformed to normalize data, as suggested by Box-Cox tests (Box and Cox 1964). Individual ANOVAs were performed for each variable to test for differences along the forest edge to interior gradient. Model quality was evaluated using whole-model ANOVA comparisons (Pinheiro and Bates 2000) and by comparing the standard deviation of the model’s residuals to the standard deviation of the variable of interest.

Results

Within-leaf $\delta^{13}C$ variation

No significant within-leaf variability was detected in the $\delta^{13}C$ value of leaflets from the bottom, middle, and top of *P. macroloba* leaves ($p = 0.89$) (Table 1). However, a small difference in sub-leaflet $\delta^{13}C$ values was detected ($p = 0.03$), with sub-leaflets at the base of the leaflet more depleted than those at the tip (mean difference: -0.16‰) (Table 1). It should be noted that this difference was below the level of precision in analyzed duplicate foliar samples (0.25‰).

Forest edge to interior gradients

$\delta^{13}C_{leaf}$ and WUE

$\delta^{13}C_{leaf}$ was invariant along the forest edge to interior gradient for both canopy ($p = 0.80$) and understory foliage ($p = 0.28$) (Fig. 1). The mean $\delta^{13}C_{leaf}$ for canopy foliage was -29.65 ± 0.07‰ and was -32.51 ± 0.08‰ for understory foliage.

Given the influence of VPD, estimates of WUE were somewhat more variable than $\delta^{13}C_{leaf}$, particularly for canopy foliage. However, no significant differences were detected along the forest edge to interior gradient for either canopy ($p = 0.16$) or understory foliage ($p = 0.81$) (Fig. 2). Mean WUE for canopy foliage was 19.7 ± 0.6 mmol mol^{-1} and was 10.8 ± 0.5 mmol mol^{-1} for understory foliage.

LMA and leaf nitrogen

No differences in LMA were detected for either canopy ($p = 0.25$) or understory ($p = 0.43$) foliage along the edge to interior gradient (Table 2). Similarly, no significant differences in N_{mass} or N_{area} were observed along this gradient for either canopy ($p = 0.44$, 0.60) or understory foliage ($p = 0.71$, 0.25) (Table 2). LMA in canopy foliage averaged 66.65 ± 0.97 g m^{-2} and was nearly double the mean LMA of understory foliage, 35.25 ± 0.69 g m^{-2} (Table 2). N_{area} was consistently higher in canopy foliage, relative to understory foliage, while the opposite was true of N_{mass}.

$\delta^{13}C_{soil}$ and $\delta^{13}C_{R\text{-}soil}$

$\delta^{13}C_{soil}$ for samples collected from the top 10 cm of mineral soil did not vary along the forest edge to interior gradient ($p = 0.16$) (Fig. 3), and the mean value across all distance classes was -27.96 ± 0.05‰. However, $\delta^{13}C_{R\text{-}soil}$ did vary significantly across the edge to interior gradient (p = 0.0347) (Fig. 3). Values were more depleted at the forest edge than in the interior and ranged from -29.24 ± 0.39‰ at 0 m to -28.57 ± 0.28‰ at 300 m.

Discussion

Aboveground responses to forest edge effects

In contrast to our expectations, we did not observe enriched $\delta^{13}C_{leaf}$ and increased WUE in canopy or understory *P. macroloba* trees growing near forest edges (Fig. 1, 2). These data indicate that water stress in the form of limited soil moisture or high evaporative demand was not a factor affecting *P. macroloba* trees at the forest edge. Studies that have investigated changes in $\delta^{13}C_{leaf}$ and/or WUE over environmental gradients have found irradiance and VPD to be significant factors in determining WUE (Ehleringer et al. 1986; Marshall and Zhang 1994; Hanba et al. 1997). However, neither of these factors appears to be influential along forest edge to interior gradients in these tropical forests.

A study of edge effects conducted five years after forest edge creation in the Brazilian Amazon also failed to find variation in the $\delta^{13}C_{leaf}$ of two canopy tree species along forest edge to interior transects (Kapos et al. 1993). However, enrichment in $\delta^{13}C_{leaf}$ was observed in an understory species at these forest edges and this was linked to both increased canopy openness at these young forest edges and enriched $\delta^{13}C$ values in understory air (Kapos et al. 1993). Fragmented forests in Sarapiquí develop edges that seal with dense vegetation in the 20-30 years following edge creation, and no difference in canopy openness has been found between edge and interior environments (Schedlbauer et al. 2007). The presence of a sealed edge decreases the likelihood that well-mixed air from outside the forest will penetrate edges and influence understory $\delta^{13}C_{leaf}$. Our understory $\delta^{13}C_{leaf}$ data are consistent with this idea (Fig. 1).

Although we did not detect evidence of edge effects in our measures of $\delta^{13}C_{leaf}$ and WUE, there exists the possibility that *P. macroloba* trees growing directly adjacent to forest edges do exhibit increased WUE. Our sampling design was such that edge plots included trees growing anywhere between 0 and 20 m from the forest edge. Trees at the immediate edge of the forest are likely subject to a more extreme environment than trees growing close to an edge. The influence of hotter, drier conditions in adjacent pastures, as well as increased crown irradiance at edges could affect tree water relations on a scale smaller than that measured in the present study. While this possibility exists, it is unlikely that it would have any significant effect on the forest as a whole. The development of dense vegetation at forest edges in Sarapiquí appears to stabilize edges (Schedlbauer et al. 2007), and the potential for increased WUE in *P. macroloba* growing at immediate forest edges is unlikely to threaten this stability.

The overall lack of variation in $\delta^{13}C_{leaf}$ within both the canopy and understory suggests that the $\delta^{13}C$ value of carbon available when leaves were developing was relatively constant. This is not surprising, given the relative aseasonality of temperature and precipitation in the Sarapiquí region (Sanford et al. 1994). Studies in tropical regions with distinct seasonality also report little to no change in $\delta^{13}C_{leaf}$ in canopy species between wet and dry seasons (Buchmann et al. 1997; Terwilliger et al. 1997).

Within individual *P. macroloba* leaves, only small variation in $\delta^{13}C$ was detected (Table 1), indicating that a random sampling of leaflets sufficiently captures the overall bulk $\delta^{13}C_{leaf}$. Further, these data show that leaflet and sub-leaflet position within *P. macroloba* leaves does not reflect differential patterns of WUE. The whole leaf appears to function simultaneously, regardless of the distance that water must travel through conducting tissue to reach different parts of the leaf.

Comparison of canopy and understory foliage

Photosynthetic capacity may influence $\delta^{13}C_{leaf}$ (Hanba et al. 1997; Duursma and Marshall 2006), and was assessed here indirectly via measures of LMA, N_{mass}, and N_{area} (Field and Mooney 1986; Reich et al. 1992; Reich et al. 1997). None of these parameters exhibited significant changes with increased distance to forest edges for either canopy or understory foliage (Table 2), indicating that differences in photosynthetic capacity were not influential in determining $\delta^{13}C_{leaf}$. However, the variation in these parameters between canopy and understory *P. macroloba* trees was important in explaining the differences in $\delta^{13}C_{leaf}$ from the canopy to the understory.

A mean difference in $\delta^{13}C_{leaf}$ of 2.86‰ was observed between canopy and understory *P. macroloba* foliage, with canopy foliage exhibiting a more enriched $\delta^{13}C_{leaf}$ than understory foliage (Fig. 1). This difference is slightly lower than the range typically reported for tropical forests (Medina and Minchin 1980; Sternberg et al. 1989; Buchmann et al. 1997), perhaps because other studies introduce interspecies variation to measures of $\delta^{13}C_{leaf}$ and we report values for one species only. Buchmann et al. (2002), in a global analysis, determined that approximately 70% of the variation in $\delta^{13}C_{leaf}$ within forest canopies is related to changes in discrimination, while the remaining 30% is attributed to variation in the $\delta^{13}C$ of source air available for photosynthesis. Of the variation related to discrimination, there is a lack of consensus regarding the strongest drivers of the gradient in $\delta^{13}C_{leaf}$ within forest canopies. However, variation in light availability as well as differences in photosynthetic capacity between canopy and understory foliage is often influential in determining $\delta^{13}C_{leaf}$ (Hanba et al. 1997; Duursma and Marshall 2006).

LMA, an index of leaf thickness, nearly doubled in canopy foliage, relative to understory foliage (Table 2). This pattern is characteristic of sun and shade foliage (Lambers et al. 1998) and reflects the difference in light availability between the canopy and understory. The high N_{area} observed in canopy foliage (Table 2) is also a manifestation of high light availability in the forest canopy, as most leaf nitrogen is associated with the photosynthetic apparatus of a leaf (Evans and Seemann 1989; Hanba et al. 1999). Although we detected higher N_{mass} in understory foliage than canopy foliage (Table 2), this pattern is likely related to the thinness of shade leaves. High WUE in canopy trees relative to understory trees is partially the result of high light availability and photosynthetic capacity, both of which lead to draw-downs in c_i. However, differences in water conducting path length, boundary layer conductance, leaf temperature, and leaf-to-air vapor pressure difference between foliage in canopy and understory trees can also influence c_i by inducing earlier or more frequent stomatal closure in canopy foliage.

Ideally, estimation of WUE from $\delta^{13}C_{leaf}$ should account for the transfer conductance of CO_2 from a leaf's substomatal cavity to the chloroplasts and the associated discrimination against ^{13}C (Evans and von Caemmerer 1996). Because the CO_2 concentration in chloroplasts is reported to be ~30% lower than c_i, transfer conductance has the potential to decrease WUE by constraining photosynthesis (Evans and von Caemmerer 1996). Any variation in transfer conductance has consequences for discrimination against $^{13}CO_2$ molecules. Leaf thickness and photosynthetic capacity are often positively correlated with transfer conductance (Evans and von Caemmerer 1996; Hanba et al. 1999; Warren et al. 2003), but neither variable was found to change along the forest edge to interior gradient in the present study (Table 2). Consequently, it is unlikely that transfer conductance varied within either canopy or understory foliage; however, variation in transfer conductance likely influenced WUE between canopy and understory foliage. Because our estimates of WUE did not account for transfer conductance, these WUE values are best viewed as a relative measure within a canopy level, and should not be directly compared between canopy and understory foliage.

Belowground responses to forest edge effects

Consistent with our hypothesis that canopy-level patterns in $\delta^{13}C_{leaf}$ would be reflected belowground, $\delta^{13}C_{soil}$ was found not to vary with distance to forest edges (Fig. 3). However, a significant depletion in $\delta^{13}C_{R\text{-}soil}$ was detected in plots close to the forest edge (Fig. 3). The magnitude of this depletion was approximately 0.5‰ and, though small, was consistent for all plots within 0-50 m of the forest edge. Evidence presented above decreases the likelihood that alterations in canopy processes such as photosynthesis and transpiration are responsible for these changes at the forest edge. Further, relatively constant $\delta^{13}C_{soil}$ along the edge to interior gradient makes it unlikely that differences in the $\delta^{13}C$ of soil organic matter explain these changes.

As described previously, the edges of forest fragments in Sarapiquí seal with vegetation in the 20-30 years following edge creation (Schedlbauer et al. 2007), a process that is likely related to an increase in pioneer species at edges (Forero and Finegan 2002). Pioneer species and shade tolerant or late-successional species in tropical forests do not vary consistently in $\delta^{13}C_{leaf}$ (Huc et al. 1994; Bonal et al. 2000a), although the direction of isotopic shifts among tree functional types often varies with the ecophysiological traits of individual species (Huc et al. 1994; Bonal et al. 2000b). In the forests of Sarapiquí, it is possible that the carbon available for root and rhizosphere respiration in pioneer species is more depleted than that of late-successional species. This depleted signal would then be evident in $\delta^{13}C_{R\text{-}soil}$ in areas of the forest dominated by early successional species, such as the forest edge. These possible shifts in $\delta^{13}C_{leaf}$ may not have been detected in $\delta^{13}C_{soil}$ because these forest edges are not occupied solely by early successional species. Further research is needed to assess whether variation in $\delta^{13}C_{leaf}$ among tree functional groups is a potential driver of patterns of $\delta^{13}C_{R\text{-}soil}$ at forest edges in Sarapiquí.

Conclusions

Forest functional changes in response to the presence of an edge were generally not detectable in the fragmented forests of Sarapiquí. Along edge to interior gradients, we did not observe significant changes in $\delta^{13}C_{leaf}$, WUE, or any measured leaf characteristics in either canopy or understory foliage. Therefore, we conclude that trees growing close to forest edges are robust and functionally similar to trees in the forest interior. Variation in $\delta^{13}C_{leaf}$, WUE, and other leaf characteristics between canopy and understory foliage was typical of patterns commonly observed in forest canopies. Consistent with our aboveground data, no differences in $\delta^{13}C_{soil}$ were found along edge to interior gradients. However, we did detect significantly greater depletion of $\delta^{13}C_{R\text{-}soil}$ at forest edges relative to interiors, but this pattern may be tied to shifts in species composition at edges rather than physiological responses to edge effects. Overall, these results are consistent with other edge effects research in Sarapiquí reporting the development of a dense wall of vegetation at these forest edges (Forero and Finegan 2002, Schedlbauer et al. 2007). This dense vegetation appears to be effective in sealing the forest edge, as we detected few forest functional changes in edge zones.

Acknowledgements

Thanks to Leonel Coto for assistance in climbing trees and also to Stacy Sesnie, Benjamin Miller, Erika Barrientos, and Bertha Gonzalez for help processing and analyzing foliage. Germán Obando and Andrés Sanchún from FUNDECOR provided logistical support for fieldwork. Thanks to the landowners in Sarapiquí who graciously permitted access to their land. Helpful reviews of an earlier version of this manuscript were provided by Bryan Finegan, John Marshall, and Paul McDaniel. This research was supported in part by NSF-IGERT grant no. 0114304. The research described in this paper complies with the current laws of Costa Rica.

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Table 1. Within-leaf variation in $\delta^{13}C$ measured for eight individual trees. Trees are identified by their crown position as either canopy (C) or understory (U). Among-leaflet variation in $\delta^{13}C$ was measured in leaflets from the bottom, middle, and top third of the leaf. Within-leaflet variation in $\delta^{13}C$ was measured at the base and tip of leaflets from the middle third of each leaf.

	Among-leaflet $\delta^{13}C$ (‰)			**Within-leaflet $\delta^{13}C$ (‰)**	
Tree	Bottom	Middle	Top	Base	Tip
C-1	-29.46	-29.48	-29.66	-29.63	-29.35
C-2	-28.37	-28.24	-28.26	-28.56	-28.60
C-3	-28.76	-28.56	-28.44	-28.66	-28.61
C-4	-29.31	-29.05	-29.01	-29.29	-28.90
C-5	-31.16	-31.07	-31.10	-30.99	-30.88
U-1	-31.20	-31.30	-31.30	-31.32	-31.27
U-2	-31.55	-31.54	-31.65	-31.56	-31.55
U-3	-31.42	-31.57	-31.71	-32.09	-31.60

Table 2. Mean LMA, N_{mass}, and N_{area} ± one standard error for canopy and understory foliage as a function of distance to the forest edge.

Distance to forest edge (m)	LMA (g m^{-2})	N_{mass} (mg g^{-1})	N_{area} (g m^{-2})
Canopy foliage			
0	68.28 ± 0.82	26.20 ± 0.62	1.79 ± 0.06
25	62.26 ± 2.29	27.35 ± 0.59	1.72 ± 0.09
50	66.29 ± 1.48	26.83 ± 0.64	1.77 ± 0.05
100	65.43 ± 1.92	26.90 ± 0.60	1.76 ± 0.07
200	69.15 ± 1.65	26.68 ± 0.70	1.84 ± 0.05
300	68.08 ± 1.46	26.12 ± 0.51	1.78 ± 0.04
Understory foliage			
0	36.67 ± 1.19	31.34 ± 0.66	1.15 ± 0.04
25	33.71 ± 0.89	31.91 ± 0.40	1.08 ± 0.03
50	35.27 ± 0.70	31.01 ± 0.71	1.10 ± 0.04
100	37.04 ± 2.07	31.95 ± 0.64	1.17 ± 0.05
200	34.72 ± 0.82	30.65 ± 0.59	1.06 ± 0.02
300	33.91 ± 0.82	31.80 ± 0.51	1.08 ± 0.03

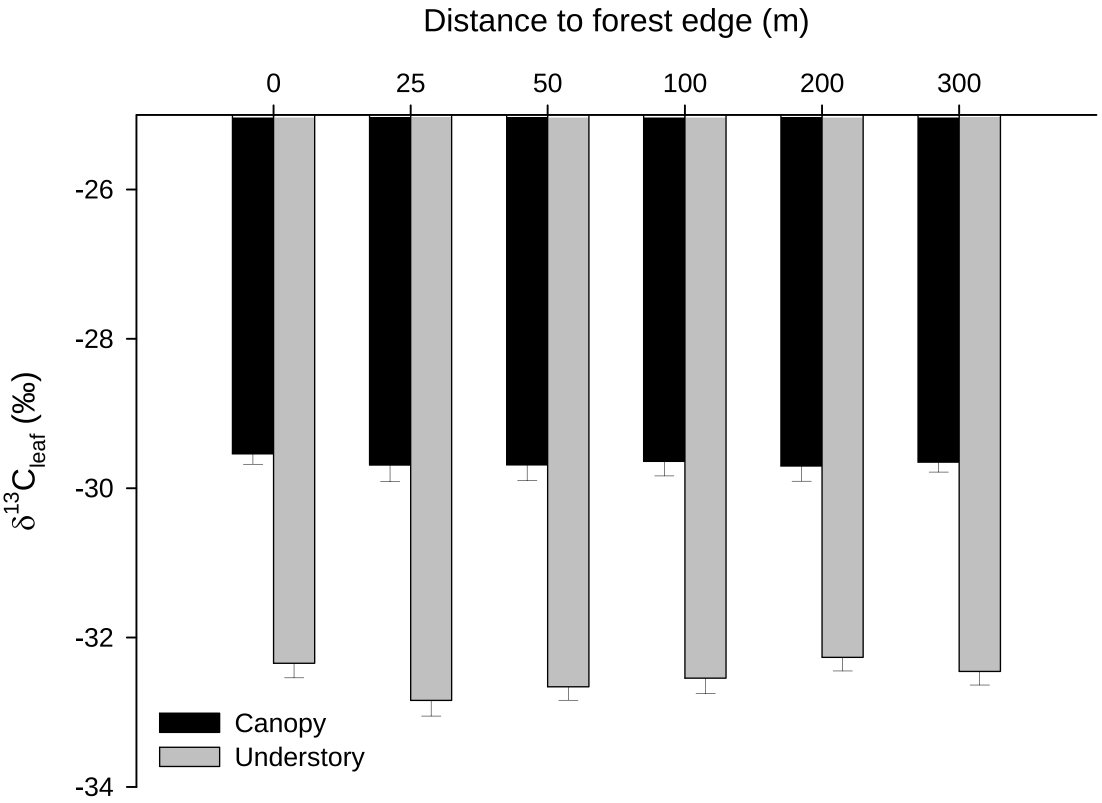

Figure 1. Mean $\delta^{13}C_{leaf}$ ± one standard error of *Pentaclethra macroloba* canopy and understory foliage as a function of distance to the forest edge.

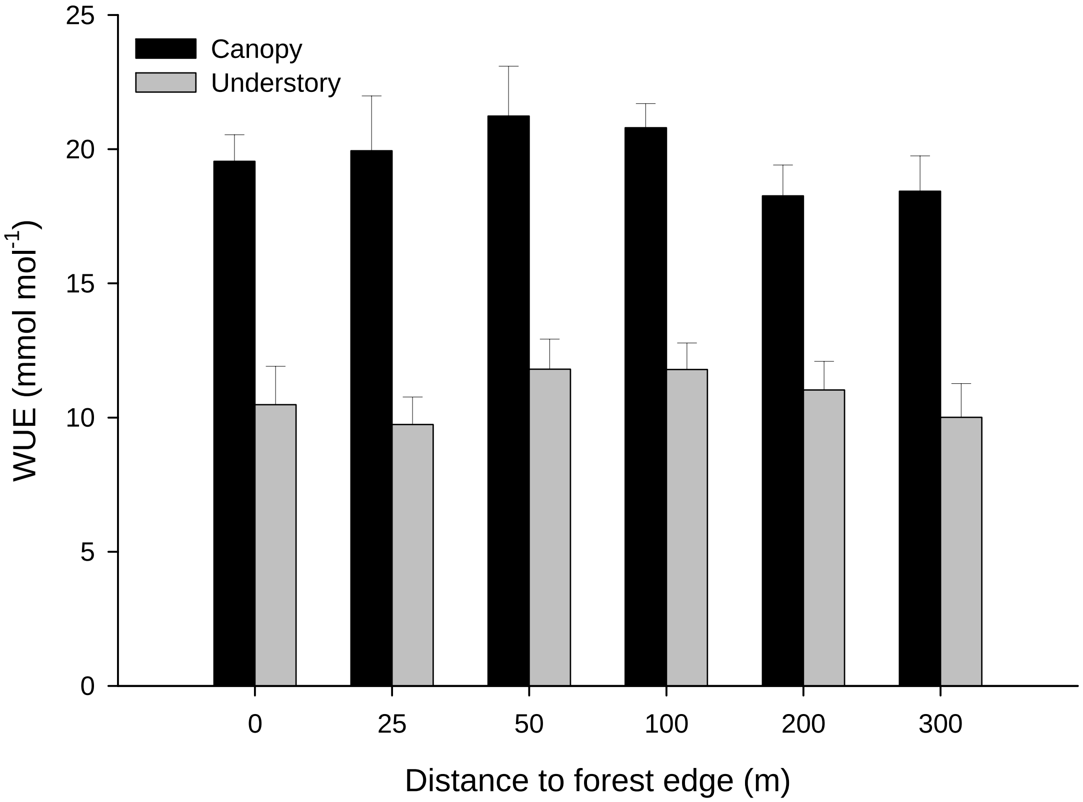

Figure 2. Estimated WUE ± one standard error for *Pentaclethra macroloba* canopy and understory foliage as a function of distance to the forest edge.

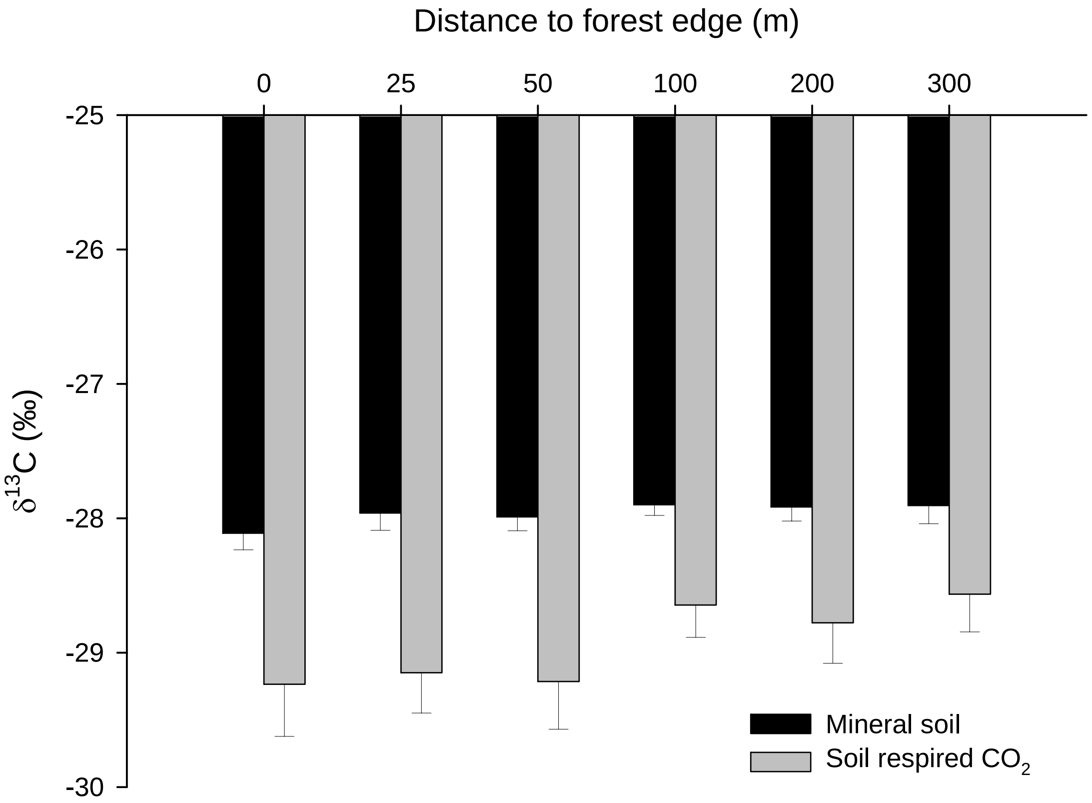

Figure 3. $\delta^{13}C_{soil}$ and $\delta^{13}C_{R\text{-}soil}$ ± one standard error as a function of distance to the forest edge.

CHAPTER 3. SOIL CARBON DYNAMICS IN A CHRONOSEQUENCE OF SECONDARY FORESTS IN NORTHEASTERN COSTA RICA

Abstract

Secondary forests are becoming an increasingly important tropical landscape component with the potential to provide environmental services such as soil carbon storage. Substantial losses of soil carbon can occur with tropical forest conversion to pasture, but stocks can sometimes be restored with the development of secondary forest. Few studies have taken advantage of shifts in vegetation from C_4 to C_3 communities to determine soil carbon turnover following secondary forest development on pasture. We expected to find evidence of gradual soil carbon turnover and an increase in soil carbon storage following pasture abandonment. Three early successional and nine late successional secondary sites ranging in age from 2.6 to 33 years, as well as four pastures were used in this study. At each site, mineral soil samples to 30 cm depth were collected from three plots to determine bulk density, percent soil carbon, and stable carbon isotope values ($\delta^{13}C$). The $\delta^{13}C$ of soil respired CO_2 was also determined at each site. Pastures stored 19% more carbon than early and late successional sites in the top 10 cm of mineral soil, though successional sites stored 14-18% more carbon than pastures between 10 and 30 cm. Contrary to expectations, soil carbon storage did not increase with secondary forest age and was unrelated to increases in aboveground carbon storage. However, $\delta^{13}C$ data showed that soil carbon in the top 30 cm of soil turned over within ten years of pasture abandonment and subsequent colonization by trees. Overall, these data indicate that soil carbon cycling can recover rapidly following pasture abandonment, though total soil carbon storage may remain unchanged. The conservation value of secondary forests within a highly fragmented landscape such as that in northeastern Costa Rica is augmented by the recovery of soil carbon cycling in these forests.

Introduction

The tropics provide a significant carbon (C) reservoir, particularly belowground, where it is estimated that the top three meters of soil beneath tropical evergreen forests store 474 Pg of C globally (Jobbágy & Jackson, 2000). This represents approximately 20% of total global soil C storage, so mobilization of soil C through land use transitions (e.g. forest to agricultural conversions) may have wide ranging impacts. The recruitment of forest following abandonment of intensively used land is often related to increased soil C storage

(Post & Kwon, 2000; Guo & Gifford, 2002), suggesting that secondary forest recruitment may significantly increase soil C stores in landscapes with widespread land abandonment.

Studies of soil C storage in tropical secondary forests are increasingly common (e.g. Hughes *et al.*, 2002; Feldpausch *et al.*, 2004), but have rarely taken advantage of stable C isotope methods to examine soil C origin and turnover. The origin of soil C following land use conversions between forests dominated by C_3 vegetation and tropical pastures or savannas with C_4 grasses can be studied using stable C isotope values ($\delta^{13}C$) in mineral soil (Ehleringer *et al.*, 2000). Because the C_3 and C_4 photosynthetic pathways discriminate differently against the heavier C isotope, ^{13}C, it is possible to determine the vegetation type from which soil organic matter is derived. Typically, studies employing these $\delta^{13}C$ data have focused on forest to pasture transitions (Trumbore *et al.*, 1995; Powers & Veldkamp, 2005) and historical ecotone dynamics (Mariotti & Peterschmidtt, 1994; Desjardins *et al.*, 1996). There have been few studies primarily concerned with secondary forest recruitment following pasture abandonment (e.g. de Camargo *et al.*, 1999; Rhoades *et al.*, 2000).

Secondary forest development has proved an important element of landscape dynamics in some tropical regions (Grau *et al.*, 2003; Arroyo-Mora *et al.*, 2005), and is likely to increase in global prominence as a landscape feature (Wright, 2005). As such, it is critical to gain an understanding of how C dynamics change in response to land abandonment and secondary forest development. However, soil C storage varies with factors such as land use history and intensity, soil mineralogy, and topography (Post & Kwon, 2000; Powers & Veldkamp, 2005), necessitating regional studies of soil C storage. These data are used in global and regional modeling of changes in C storage following land use transitions (Trumbore, 1997), but are also of local interest as monetary valuation of environmental services such as C storage becomes increasingly common (Pagiola *et al.*, 2002).

In Costa Rica, a 1996 Forestry Law (No. 7575) introduced a novel program of payments for environmental services (PES) directed toward private landowners who agree to protect natural forests or establish tree plantations. Carbon sequestration is one of the environmental services targeted by PES and was integrated into the program given its potential to raise funds and support local livelihoods as global C markets develop (Miranda *et al.*, 2004). PES contracts for natural secondary regeneration were recently incorporated into the program, but are currently confined to Guanacaste in northwestern Costa Rica, the site of large-scale pasture abandonment (Arroyo-Mora *et al.*, 2005; FONAFIFO, 2006). While regional studies of soil C dynamics in Costa Rica's secondary forests are uncommon, they are essential in quantifying C services provided by these forests. Further, these data may be valuable in guiding the future distribution of PES contracts.

Our objective was to examine mineral soil C storage and origin in secondary forests following pasture abandonment. We investigated $\delta^{13}C$ values of mineral soil ($\delta^{13}C_{soil}$) and soil respired CO_2 ($\delta^{13}C_{R\text{-}soil}$) relative to secondary forest age. A chronosequence of naturally regenerating secondary forest sites spanning 30+ years of development was used for this purpose. We expected to find evidence of forest recovery toward primary forest conditions by means of increased soil C storage and a gradual rise in C_3-derived C as secondary forests developed on abandoned pastures.

Methods

Study Region

This study was conducted in the Sarapiquí region of northeastern Costa Rica, an area primarily classified as tropical wet forest by the Holdridge life zone system (Tosi, 1969). Mean annual rainfall in the region is ~4000 mm and annual temperatures average 26°C with little seasonal variation (Sanford *et al.*, 1994). The landscape in Sarapiquí consists primarily of fragmented forests with interspersed pasture and crop land.

Field Sites and Chronosequence Approach

A chronosequence of twelve secondary forest sites was used in this study, and all sites had a previous land use history as pasture (Table 1). Sites ranged in age from 2.6 to 33 years, with age 0 as the date of pasture abandonment. Three sites, C-2.6, C-2.8, and C-7, were in the early-successional *charral* phase of development, characterized by shrubs, vines, grass, ferns, and herbaceous cover. The nine older sites were all tree dominated and eligible for legal classification as forest under Costa Rica's 1996 Forestry Law. Four pastures ≥ 18 years old with a grazing intensity of 1-2 cows per ha were also selected for sampling (Table 1). Study sites ranged in elevation from 60 to 330 m a.s.l. and were characterized by low, undulating hills. All sites but one were located on acidic, highly weathered Ultisols (Tropohumult) derived from volcanic parent material (ITCR 2004). The oldest secondary forest site, SF-33, was located on an acidic Inceptisol (Dystropept) with low fertility derived from alluvial deposits of volcanic origin (ITCR 2004).

In employing a space-for-time substitution to study secondary forest C storage and cycling, differences among sites may introduce variation unrelated to secondary development (Yani *et al.*, 2000; Yani *et al.*, 2003). However, sites were carefully chosen from within a 224 km^2 area to minimize differences among variables such as land use history and topography. Chronosequence approaches are efficient in determining the potential of secondary forests to recover biogeochemical cycles, relative to alternative approaches. Several decades are necessary to complete repeated measures studies of naturally regenerating forests, and while this approach may reduce variation, the expense and time commitment is often prohibitive. Well-chosen sites within a chronosequence can yield valuable data within a short period of time.

Soil Sampling

At each site we established three randomly located plot centers separated by at least 30 m. Within a 5 m radius of each plot center, soil samples were collected using a 6.35 cm diameter soil core sampler and slide hammer (AMS Inc., American Falls, ID, USA). When present, the litter layer was removed prior to sampling of mineral soil. Samples were taken from four locations around the plot center at 0-10, 10-20, and 20-30 cm depths. Three samples per depth were composited for $\delta^{13}C$ and % soil C determination, and the fourth sample was used for bulk density determination. All soil samples were air dried, and bulk density samples were further oven dried for 48 hours at 70°C to remove residual moisture. Bulk density samples were weighed to the nearest hundredth of a gram and no correction was made for gravel because it was extremely rare in these soils. All soil samples tested negative for the presence of carbonates using 1.0 M HCl.

Composited soil samples from each plot were sieved through a 2 mm mesh screen to remove fine roots, and subsamples of the homogenized soils were crushed into a fine powder. $\delta^{13}C_{soil}$ and % C content were determined by continuous-flow isotope ratio mass spectrometry (CF-IRMS) using a CE Instrument's NC2500 elemental analyzer coupled with the Finnigan MAT Delta-plus IRMS (Thermo Electron Corporation, Bremen, Germany) at the Idaho Stable Isotopes Laboratory (ISIL). Stable C isotope data are reported in delta notation as follows,

$$\delta^{13}C = (R_{sample} / R_{standard} - 1) \times 1000$$

where R is the ratio of ^{13}C to ^{12}C in the sample vs. a standard (PDB). Fifteen duplicate soil samples were analyzed and showed a mean difference of 0.25‰.

For bulk density determination, volume corrections of 98.4% and 95.9% of the intended sample volume were applied at the 10-20 and 20-30 cm depths, respectively, due to sampling induced compaction. Corrected soil volumes were used to calculate bulk density at those depths. No compaction occurred at the 0-10 cm depth. Soil C concentrations were multiplied by bulk density, sampling depth, and an area conversion factor to express measures of soil C content in Mg C ha^{-1}.

Soil Respired CO_2 Sampling

At each site, chambers used to sample soil respired CO_2 were placed at the three plot centers. Chambers were constructed from 9-L plastic pans with a hole drilled in the pan bottom. A threaded brass coupling fitted with a compression nut and rubber septum was screwed into the hole and sealed with silicone on the exterior side of the pan. To install chambers, vegetation beneath the chamber was clipped to the ground to eliminate any aboveground respiratory inputs. A shallow circle was gently excavated in the soil, over which the chamber was inverted. Care was taken not to disturb any roots. Soil from outside the study area was placed around the base of the chamber to minimize diffusion of atmospheric air into the chamber.

Preliminary testing indicated that chambers equilibrated with soil air within four days of placement on the soil surface (data not shown). Chambers were therefore left on the soil surface for a minimum of five days, at which time a 15 ml air sample was drawn into a syringe. Air samples were injected into evacuated 12 ml septum-capped glass vials (Labco® Exetainer, Labco Limited, High Wycombe, UK) and sent to the ISIL for analysis of $\delta^{13}C$ and CO_2 concentration ([CO_2]). Samples were analyzed three to eight days after collection with CF-IRMS, using Finnigan MAT's GasBench II coupled with the Finnigan MAT Delta-plus-XP IRMS.

It was expected that all samples contained a mixture of atmospheric and soil respired CO_2 because a portion of the CO_2 in soil profiles is of atmospheric origin (Cerling *et al.*, 1991). Therefore, a Keeling plot approach was used to estimate the $\delta^{13}C$ values of pure respired CO_2 (Steinmann *et al.*, 2004). Individual Keeling plots for each chamber measurement were generated by plotting $\delta^{13}C$ vs. the inverse of [CO_2] using two points; one from the sample and the other from well-mixed atmospheric air with a $\delta^{13}C$ value of -8‰ and [CO_2] of 377 ppm (Keeling & Whorf, 2005). The linear relationship between these variables was used to determine the true isotopic composition of the respired CO_2. This value was derived from each regression's y-intercept and was further corrected by -4.4‰ to account for the difference in diffusion rates between $^{13}CO_2$ and $^{12}CO_2$ molecules in the soil matrix (Cerling *et al.*, 1991) to yield $\delta^{13}C_{R\text{-soil}}$.

Data Analyses

Statistical analyses were not performed to examine changes in soil C storage, $\delta^{13}C_{soil}$, or $\delta^{13}C_{R\text{-soil}}$ relative to site age. Our measurements represent subsamples from one site per age category, and this characteristic precludes the application of analysis of variance (ANOVA). However, we modeled $\delta^{13}C_{soil}$ at all three soil depths relative to increased site age with the logistic growth model,

$$y = (\beta_0 \times \beta_1) / (\beta_0 + (\beta_1 - \beta_0) \exp(-\beta_2 \times x))$$

where y is $\delta^{13}C_{soil}$, x is site age, β_0 is the y-intercept, β_1 is the asymptote, and β_2 indicates the maximum rate of change. Site means from each pasture, *charral*, and secondary forest site were used to create these models. The statistical language R (version 2.0.1, R Core Development Team 2004) was used for all modeling.

Results

Soil Carbon Storage

Between 0 and 10 cm, % soil C (Table 2) and mineral soil C storage (Fig. 1a) were variable with no clear pattern of increased C storage coincident with successional development. This was also true at depths of 10-20 and 20-30 cm, though within-site variation declined with increased soil depth (Table 2, Fig. 1b, c). Relative to pasture, soils under natural regeneration stored a slightly lower amount of soil C between 0 and 10 cm (Fig. 1a). Increased soil C storage in regenerating stands, relative to pasture, was detected between 10 and 30 cm depth (Fig. 1b, c). From 0-30 cm, *charral* and secondary forests stored an average of 49% of total soil C in the top 10 cm, with decreased concentrations at 10-20 (30%) and 20-30 (21%) cm depths. Increases in aboveground C storage reported at the nine secondary forest sites after ~25 years of development (Morse *et al.*, unpublished manuscript) were not related to any changes in mineral soil C storage (Fig. 2).

$\delta^{13}C_{soil}$

$\delta^{13}C_{soil}$ in secondary sites decreased rapidly with time following pasture abandonment at all soil depths (Fig. 3). Because the three youngest sites were *charrals*, they contained transitional vegetation between pasture and secondary forest. As such, these sites had $\delta^{13}C_{soil}$ values similar to those found in pasture. Following establishment of tree cover on secondary sites, the $\delta^{13}C_{soil}$ between 0 and 10 cm depth became more depleted than values derived from *charral* or pasture. However, these values did not change with increased secondary forest age. At 10-20 and 20-30 cm soil depths, $\delta^{13}C_{soil}$ from all sites began to converge, although secondary forest sites had a consistently more depleted signal than pasture (Fig. 3 b, c). Within-site variation in $\delta^{13}C_{soil}$ was higher in *charrals* than in secondary forest sites (Fig. 3). As observed in the soil C data, within-site variation declined with increased depth.

Logistic growth models showed a gradual enrichment in the value denoting the model's asymptote (β_1) with increased soil depth (Table 3). The y-intercept (β_0) was more depleted with increased depth, while the maximum rate of change (β_2) was similar and had large standard errors for all soil depths (Table 3).

$\delta^{13}C_{R\text{-}soil}$

$\delta^{13}C_{R\text{-}soil}$ values followed a similar pattern to those observed for mineral soil. *Charral* sites had more enriched $\delta^{13}C_{R\text{-}soil}$ than secondary forest sites (Fig. 4). The value for C-7 in particular was very close to the mean $\delta^{13}C_{R\text{-}soil}$ in pastures. This was likely because C-7 contained more grass than either of the other *charral* sites. As with the soils data, secondary forest sites varied little in $\delta^{13}C_{R\text{-}soil}$ once trees were established, and these sites had a mean $\delta^{13}C_{R\text{-}soil}$ of -30.08 ± 0.09‰ (± values indicate one standard error throughout the text). $\delta^{13}C_{R\text{-}soil}$ was consistently more depleted than $\delta^{13}C_{soil}$ at all depths in all secondary forest and most *charral* sites (Fig. 5). The opposite tended to be true for pasture sites, with $\delta^{13}C_{R\text{-}soil}$ more enriched than $\delta^{13}C_{soil}$ (Fig. 5).

Discussion

Soil Carbon Storage

In contrast with our expectations, soil C storage in secondary forests from 0-30 cm did not increase with age. Increased leaf litter inputs commonly associated with secondary forest development (Brown & Lugo, 1990a, b; Guariguata & Ostertag, 2001) did not lead to an increase in soil C stocks. Within each depth class, secondary forest soil C storage was roughly the same through time (Fig. 1) and did not show any relationship with increased aboveground C storage (Fig. 2). Although a lack of soil C accumulation with increased forest age is not common in the tropics (Brown & Lugo, 1990a; Rhoades *et al.*, 2000; Feldpausch *et al.*, 2004), it has been previously reported (Hughes *et al.*, 1999).

Recent evidence from the Sarapiquí region suggests that changes in soil C storage following forest to pasture conversions are not detectable in the top 30 cm of soil. Powers & Veldkamp (2005) found that mean values of mineral soil C storage were similar in primary forest (80.5 Mg C ha^{-1}) and pasture (76.7 Mg C ha^{-1}), though variation was high and best explained by topographic features and soil mineralogy. In the present study, mineral soil C content from 0-30 cm depth in pastures was 75.0 Mg C ha^{-1}, while in *charral* and secondary forest sites it was 72.5 Mg C ha^{-1}. These small differences between land use types are consistent with changes found following conversion of primary forest to pasture.

An additional study of forest to pasture conversion in Sarapiquí showed no change in mineral soil C content at 0-30 cm depth in highly weathered soils derived from lava flows (Veldkamp *et al.*, 2003). As deforestation is reversed and natural regeneration begins, it follows that a significant increase in mineral soil C may not occur in these soils. We confined our study sites to old volcanic soils in Sarapiquí, so it is not surprising that our data are consistent with the pattern observed by Veldkamp *et al.* (2003). While the top 30 cm of volcanic mineral soils may stabilize a fairly consistent amount of C through land use transitions, data from Sarapiquí that show that soil C losses of 20+% occur in the subsoil (>1 m depth) following forest to pasture conversion (Veldkamp *et al.*, 2003). Further study will be essential in quantifying the effects of secondary forest recovery on soil C dynamics in deep soils.

Factors associated with soil mineralogy may be responsible for the relatively consistent amount of C stored in surface soils under developing secondary forests. In Sarapiquí, Powers & Schlesinger (2002) found soil C stabilization occurring at low elevation sites from aluminum – humus linkages, while noncrystalline clays were active in C stabilization at sites above 120 m. Both of these mineralogical properties are associated with high C storage capacity and may reduce C losses in surface soils following land use transitions. Hughes *et al.* (1999) suggested that the substantial soil C storage capacity of young volcanic soils was responsible for a similar pattern of stable soil C storage in developing secondary forests of Los Tuxtlas, Mexico.

Although the amount of C stored in surface mineral soils was relatively unvarying following land use transitions, the distribution of C in the soil profile appeared to change with the source of detrital inputs (i.e., leaf litter, shallow vs. deep roots) (Jackson *et al.*, 1996; Jobbágy & Jackson, 2000). Pastures stored 19% more soil C in the top 10 cm of mineral soil than *charrals* or secondary forests, perhaps as a result of high fine root density in pasture, relative to forest (Rhoades *et al.*, 2000; Powers & Veldkamp, 2005). As natural regeneration proceeded and pastures became colonized by more deeply rooted species with higher leaf litter inputs, soil C storage at depths of 10-30 cm increased relative to pasture. Specifically, *charral* and secondary forest sites stored 14 and 18% more soil C at depths of 10-20 and 20-30 cm, respectively.

$\delta^{13}C_{soil}$

Recovery of soil C cycling in secondary forests occurs rapidly in the Sarapiquí region of Costa Rica. Although we expected a gradual decline in secondary forest $\delta^{13}C_{soil}$ as time since pasture abandonment increased, this was not the case. Once naturally regenerating sites became dominated by trees and C inputs to the system were predominantly from C_3 vegetation, the C_4 $\delta^{13}C$ signal rapidly diminished (Fig. 3). In the top 10 cm of soil, the mean $\delta^{13}C_{soil}$ in secondary forests was -27.21 ± 0.07‰, while the modeled asymptote of $\delta^{13}C_{soil}$ was -27.87 ± 1.35‰ (Table 3). The agreement of these values and their similarity to the mean $\delta^{13}C_{soil}$ found in Sarapiquí's primary forests, -27.96 ± 0.05‰ (J.L. Schedlbauer, unpublished manuscript), indicate that most pasture-derived C rapidly turned over in the top 10 cm of secondary forest mineral soil. In the Brazilian Amazon, data from a study of C turnover rates, rather than a chronosequence, also showed that secondary forests rapidly turn over C in the top 10 cm of soil (de Camargo *et al.*, 1999). However, these results are contrary to those found in secondary forests of the Ecuadorian Amazon where $\delta^{13}C_{soil}$ slowly declined with increased secondary forest age (López-Ulloa *et al.*, 2005). These differences are suggestive of variable soil C dynamics following land use change across soil types and ecosystems.

We did not observe any effects of land use history in the secondary forest $\delta^{13}C_{soil}$ data. Soils in secondary forest sites known to have been used as active pasture for 3-6 years (SF-28 and SF-33) had similar $\delta^{13}C_{soil}$ values as sites that spent ~20 years as pasture (SF-22 and SF-23) at all depths (Table 1, Fig. 3). As is the case in numerous tropical forest sites (de Camargo *et al.*, 1999; Rhoades *et al.*, 2000; Telles *et al.*, 2003), we observed the classical pattern of mineral soil ^{13}C enrichment with depth in all secondary forest sites. This pattern is commonly attributed to some combination of the Suess effect, favored decomposition of isotopically light C by microbes, microbial fractionation during decomposition, and mixing of soil C in the profile through time (Ehleringer *et al.*, 2000).

We anticipated gradual depletion in $\delta^{13}C_{soil}$ with increased secondary forest age, relative to pasture. This pattern was observed only in the early-successional *charrals* where $\delta^{13}C_{soil}$ declined with increased age since pasture abandonment (Fig. 3). However, $\delta^{13}C_{soil}$ in the two youngest *charrals* was consistently more enriched than the mean value for pasture sites at all soil depths. This pattern cannot be explained by land use history effects, as both of these *charrals* spent ~22 years as managed pasture, and pasture sites were 18-25 years old. Instead, the enrichment in $\delta^{13}C_{soil}$ at these *charral* sites may be due to variation in species composition and the mix of C_3 and C_4 plants at these sites. Natural variation among sites may influence $\delta^{13}C_{soil}$ at the time of pasture abandonment. Overall, the pattern of *charral* $\delta^{13}C_{soil}$ observed with depth was most consistent with that found in pasture. This is not surprising, given that *charrals* contain a heterogeneous mixture of C_3 and C_4 vegetation. Further, it is likely that this heterogeneity contributed to the large standard errors associated with $\delta^{13}C_{soil}$ in the three *charral* sites, relative to secondary forest (Fig. 3).

The mean value of $\delta^{13}C_{soil}$ reported for pastures from 0-10 cm depth is lower than would be expected in a system with pure C_4 vegetation. The $\delta^{13}C$ value of leaf litter inputs from C_4 vegetation typically ranges from -11 to -13‰ (Cerling *et al.*, 1997). Pastures in Sarapiquí contain a mixture of grasses, woody species, and remnant trees, resulting in a mixed $\delta^{13}C$ signal that reflects the vegetation composition (Powers & Veldkamp, 2005). Additionally, the age of pastures in Sarapiquí has been positively related to $\delta^{13}C_{soil}$ in sites between 3 and 60 years old (Powers and Veldkamp 2005). It is therefore likely that the 18-25 year old pastures sampled in this study contained old forest-derived soil C that contributed to the relatively depleted $\delta^{13}C_{soil}$ signal. This conclusion is corroborated by the observed depletion in pasture $\delta^{13}C_{soil}$ with depth (Fig. 3), a pattern commonly observed in pastures and savannas previously dominated by C_3 vegetation (Martin *et al.*, 1990; Rhoades *et al.*, 2000). This pattern has been related to the persistence of resistant C_3 forest-derived C in the soil.

Additional data from pastures and secondary successional sites would advance our understanding of soil C turnover with increased successional age in tropical forests. In particular, the logistic growth models used to describe the relationship between $\delta^{13}C_{soil}$ and site age could be improved by the inclusion of old pasture sites, in which $\delta^{13}C_{soil}$ had stabilized. The addition of more sampling sites in early stages of secondary forest succession, where the highest variation and fastest rate change in $\delta^{13}C_{soil}$ were observed (Fig. 3), would contribute to a better understanding of how quickly soil C turns over in these systems.

$\delta^{13}C_{R\text{-}soil}$

Across sites, soil respired CO_2 data showed a similar isotopic pattern to that detected in the top 10 cm of mineral soil (Fig. 4). This was not unexpected because, while measures of soil respired CO_2 reflect a mixture of heterotrophic and autotrophic respiration, the transition from a C_4 to a C_3 dominated system should be evident. Secondary forest sites had a mean $\delta^{13}C_{R\text{-}soil}$ of -30.08 ± 0.09‰, consistent with expectations for sites dominated by C_3 vegetation. The low variation in this value following tree establishment in regenerating sites was consistent with the $\delta^{13}C_{soil}$ data. $\delta^{13}C_{R\text{-}soil}$ in *charrals* was intermediate between those of pasture and forest due to their mixed vegetation, and the $\delta^{13}C_{R\text{-}soil}$ in pasture reflected a strong influence of C_4 vegetation.

In comparison with $\delta^{13}C_{soil}$ data from 0-10 cm in secondary forests, $\delta^{13}C_{R\text{-}soil}$ values were nearly 3‰ more depleted (Fig. 3a, 4). This is a strong indication that the C being turned over in these forests is of C_3 origin and is consistent with data from mature forests in the Brazilian Amazon (Trumbore *et al.*, 2006). Soil respired CO_2 in *charrals* tended to have a more depleted $\delta^{13}C_{R\text{-}soil}$ than was observed in the top 10 cm of mineral soil. These data suggest that root respiration by C_3 plants or the decomposition of new C_3 organic material strongly influenced the respiratory signal. It was surprising that the signal from C_4 organic material decomposition was not more prominent in *charral* sites, in light of the rapid loss of a C_4 mineral soil signal in developing secondary forests. The $\delta^{13}C_{R\text{-}soil}$ in pastures was ~1‰ more enriched than of the top 10 cm of mineral soil, likely reflecting the influence of root respiration from C_4 plants.

In general, the $\delta^{13}C_{R\text{-soil}}$ was a poor predictor of $\delta^{13}C_{soil}$ within and across land use types (Fig. 5). It appears that root and rhizosphere respiration by the dominant vegetation type is of central importance in determining $\delta^{13}C_{R\text{-soil}}$. This observation is supported by data from Trumbore *et al.* (2006) that show the $\delta^{13}C$ values of soil CO_2 and roots to be more similar than those of soil CO_2 and soil organic matter.

Chronosequence Approach

Variation among sites for reasons unrelated to site age can introduce error when using a chronosequence approach to study dynamic processes (Yani *et al.*, 2000; Yani *et al.*, 2003). In the present study, variation in land use history was likely the most significant factor affecting the variables of interest. The length of time each site was used as pasture, as well as grazing intensity and management practices may have long-term effects on mineral soil C storage and $\delta^{13}C$ data. Site factors such as landscape composition, aspect, slope, elevation, and soil type may also locally influence mineral soil C storage, $\delta^{13}C_{soil}$, and $\delta^{13}C_{R\text{-soil}}$. The number and diversity of factors that may vary among sites within a chronosequence highlight the need for detailed time series measurements within individual sites, as suggested by Chazdon *et al.* (in press).

Conclusions

Mineral soil C storage beneath secondary forests was fairly consistent as forest development progressed. The total amount of C in soils following pasture abandonment was relatively unchanged, but the distribution of soil C shifted, with increased C accumulation at 10-30 cm in *charral* and secondary forest sites, relative to pasture. Pasture-derived C was rapidly lost in naturally regenerating stands. After ~10 years, soil C cycling resembled that of a C_3-dominated forest, as evidenced by both $\delta^{13}C_{soil}$ and $\delta^{13}C_{R\text{-soil}}$ values. The relatively rapid recovery of the soil C cycle following pasture abandonment highlights one of the values of secondary forest.

In a highly fragmented and heterogeneous landscape, such as that of Sarapiquí, secondary forests have the potential to provide C services while contributing to other conservation objectives such as biodiversity conservation and forest connectivity. These forests develop naturally with little to no human intervention, and are protected by Costa Rican law once established. Unfortunately few incentives exist to promote the establishment of secondary forest in Sarapiquí while more profitable land uses exist. We suggest that further targeting of

Costa Rica's PES program to support natural regeneration in Sarapiquí would have positive benefits for C cycling and other environmental services across the landscape.

Acknowledgements

Thanks to Edwin Pereira, Marvin Zamora, Vicente Herra, and José Manuel Ulate for assistance in the field. Germán Obando and Andrés Sanchún, both of FUNDECOR, helped greatly to facilitate fieldwork. Laboratory assistance was provided by Bob Brander, Yaneth Sanchez, and Jennifer Nalder. Thanks to Robin Chazdon and Juan Pablo Arroyo for contributing data from their secondary forest plots and allowing us to share their field sites. Bryan Finegan, John Marshall, Paul McDaniel, and Steve Blecker provided helpful reviews of earlier versions of this manuscript. Thanks to numerous landowners in the study area for providing access to their farms and forests. This research was supported in part by NSF-IGERT grant no. 0114304.

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Table 1. Site history information for all study sites in the chronosequence of secondary succession. Site names denoted by "P" are pasture sites, those denoted by "C" are in the *charral* successional phase and those denoted by "SF" are secondary forest sites. Site age refers to the number of years since pasture abandonment. Site age and estimated time as managed pasture were determined through informal interviews with landowners and examination of historical aerial photographs.

Site Name	Site age (years)	Estimated time as managed pasture (years)	Location (Lat, Long)
P1-0	0	18	10°42'N, 84°10'W
P2-0	0	25	10°43'N, 84°8'W
P3-0	0	>20	10°46'N, 84°6'W
P4-0	0	20	10°43'N, 84°9'W
C-2.6	2.6	22	10°36'N, 84°10'W
C-2.8	2.8	22	10°37'N, 84°11'W
C-7	7	>12	10°47'N, 84°6'W
SF-8	8	<5	10°47'N, 84°5'W
SF-11	11	9	10°46'N, 84°6'W
SF-15	15	12	10°46'N, 84°1'W
SF-17	17	5	10°45'N, 84°7'W
SF-20	20	2-3	10°41'N, 84°3'W
SF-22	22	~20	10°46'N, 84°6'W
SF-23	23	~20	10°40'N, 84°11'W
SF-28	28	4-6	10°43'N, 84°3'W
SF-33	33	3-5	10°39'N, 84°13'W

Table 2. Mean ± one standard error of mineral soil carbon storage (% C) for each study site and sampling depth.

	% Soil C		
Site Name	0-10 cm	10-20 cm	20-30 cm
P1-0	5.98 ± 0.69	3.40 ± 0.29	2.20 ± 0.20
P2-0	5.79 ± 0.39	2.66 ± 0.24	2.01 ± 0.22
P3-0	3.56 ± 0.24	1.82 ± 0.37	1.59 ± 0.21
P4-0	7.12 ± 0.88	3.69 ± 0.31	2.28 ± 0.14
C-2.6	5.98 ± 0.05	3.68 ± 0.28	2.40 ± 0.23
C-2.8	5.29 ± 0.87	3.08 ± 0.76	2.09 ± 0.33
C-7	5.39 ± 0.34	3.51 ± 0.39	2.76 ± 0.15
SF-8	5.54 ± 0.90	2.89 ± 0.42	1.97 ± 0.21
SF-11	4.70 ± 0.19	3.50 ± 0.26	2.48 ± 0.29
SF-15	6.19 ± 0.04	2.80 ± 0.05	2.12 ± 0.14
SF-17	6.67 ± 0.50	4.43 ± 0.48	3.70 ± 0.43
SF-20	4.60 ± 0.52	3.04 ± 0.44	2.18 ± 0.41
SF-22	5.78 ± 0.28	3.72 ± 0.13	2.90 ± 0.25
SF-23	6.62 ± 0.56	3.71 ± 0.15	2.89 ± 0.31
SF-28	6.05 ± 0.42	4.02 ± 0.25	2.86 ± 0.06
SF-33	5.55 ± 0.46	3.25 ± 0.21	2.48 ± 0.10

Table 3. Parameter estimates and standard errors for the logistic growth model used to predict mineral soil $\delta^{13}C$ over time at each soil depth.

	β_0		β_1		β_2	
Soil depth (cm)	Parameter estimate	SE	Parameter estimate	SE	Parameter estimate	SE
0-10	-21.56	0.80	-27.87	1.35	0.12	0.07
10-20	-23.70	0.52	-26.71	1.16	0.09	0.09
20-30	-24.41	0.33	-26.16	0.61	0.10	0.10

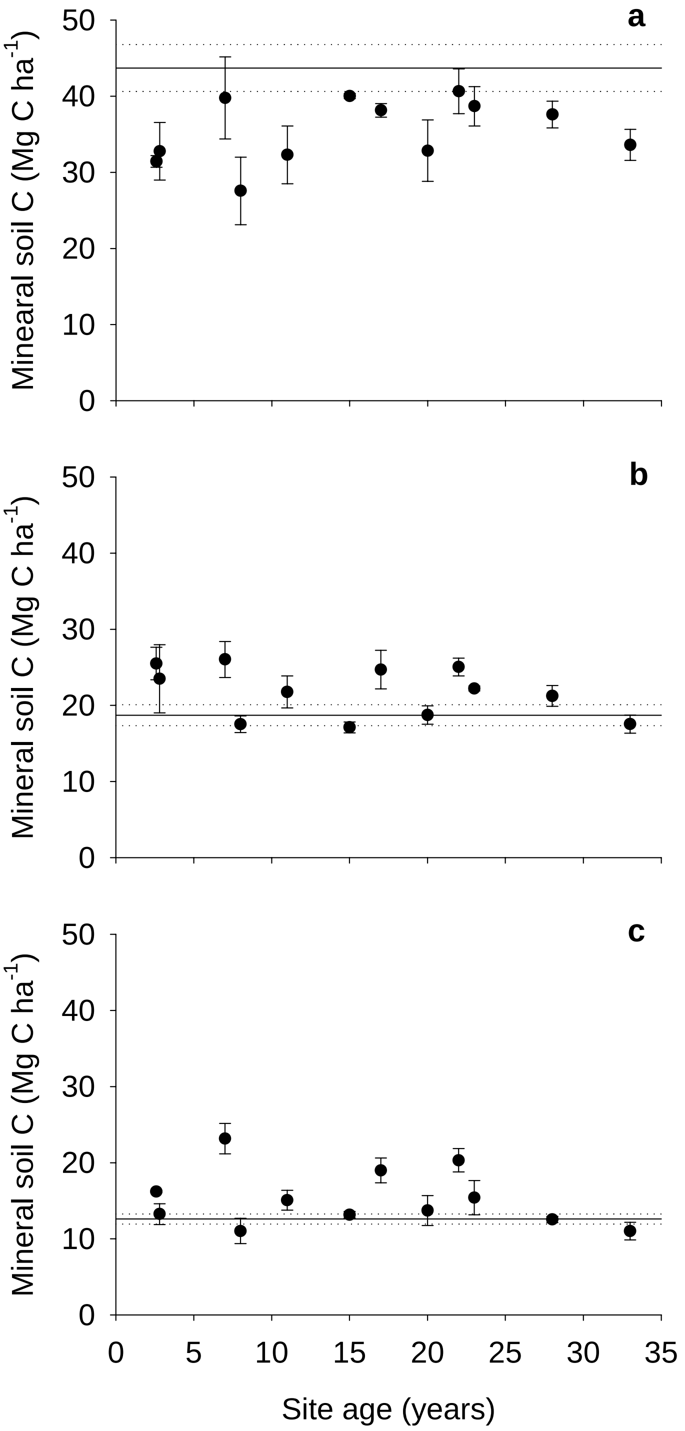

Figure 1. Mean mineral soil carbon storage ± one standard error for *charral* and secondary forest sites at soil depths of (a) 0-10, (b) 10-20, and (c) 20-30 cm. The solid horizontal lines indicate mean soil carbon storage in pasture at the given depth with ± one standard error represented by dotted lines.

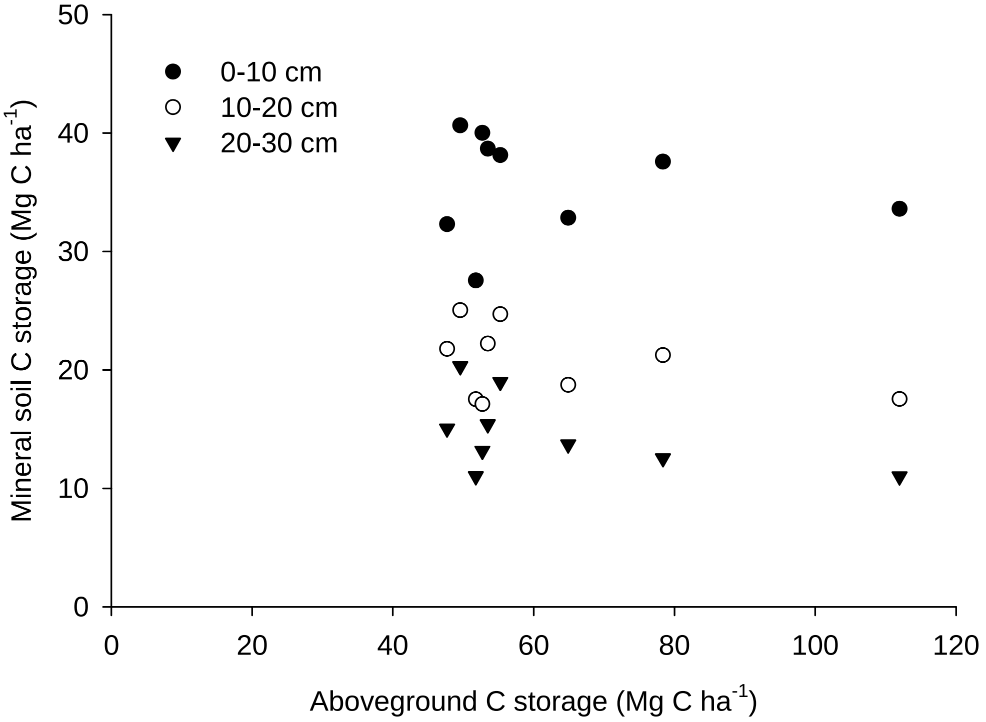

Figure 2. Mean mineral soil carbon storage at each of the three soil depths (0-10, 10-20, and 20-30 cm) plotted against mean aboveground carbon storage in the nine secondary forest sites. Aboveground values were derived from the measurement of all stems ≥ 5 cm dbh in three 50×50 m plots per site. An allometric equation (Chave et al. 2005) was used to estimate aboveground biomass, a value that was halved to approximate aboveground carbon storage.

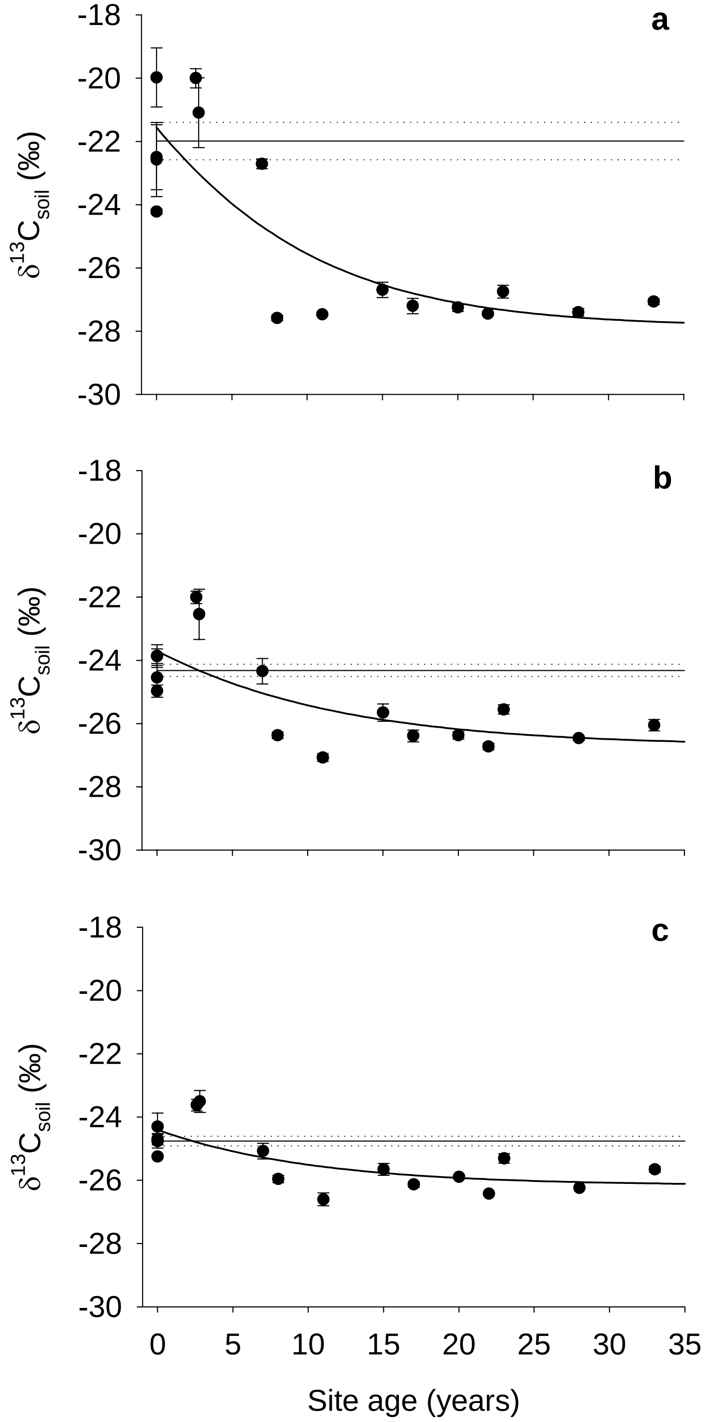

Figure 3. Mean mineral soil $\delta^{13}C$ ($\delta^{13}C_{soil}$) ± one standard error for *charral* and secondary forest sites at soil depths of (a) 0-10, (b) 10-20, and (c) 20-30 cm. The solid horizontal lines indicate mean $\delta^{13}C_{soil}$ in pasture at the given depth with ± one standard error represented by dotted lines.

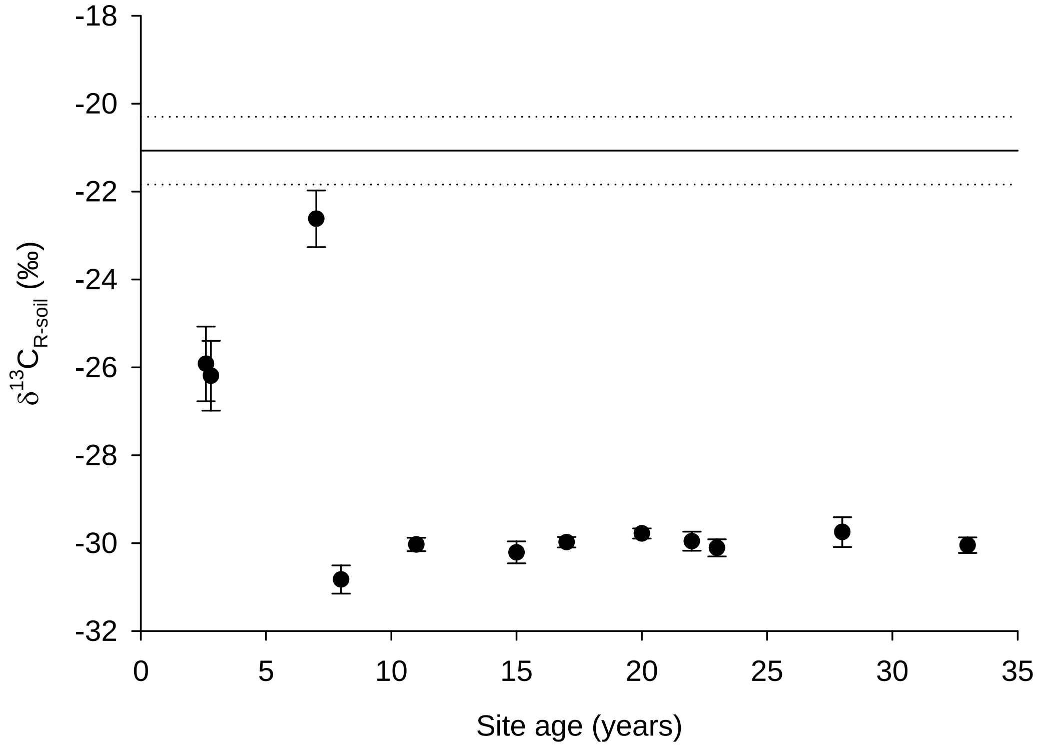

Figure 4. Mean δ^{13}C of soil respired CO_2 ($\delta^{13}C_{R\text{-soil}}$) ± one standard error for all *charral* and secondary forest sites. The solid horizontal line indicates mean $\delta^{13}C_{R\text{-soil}}$ in pasture with ± one standard error represented by dotted lines.

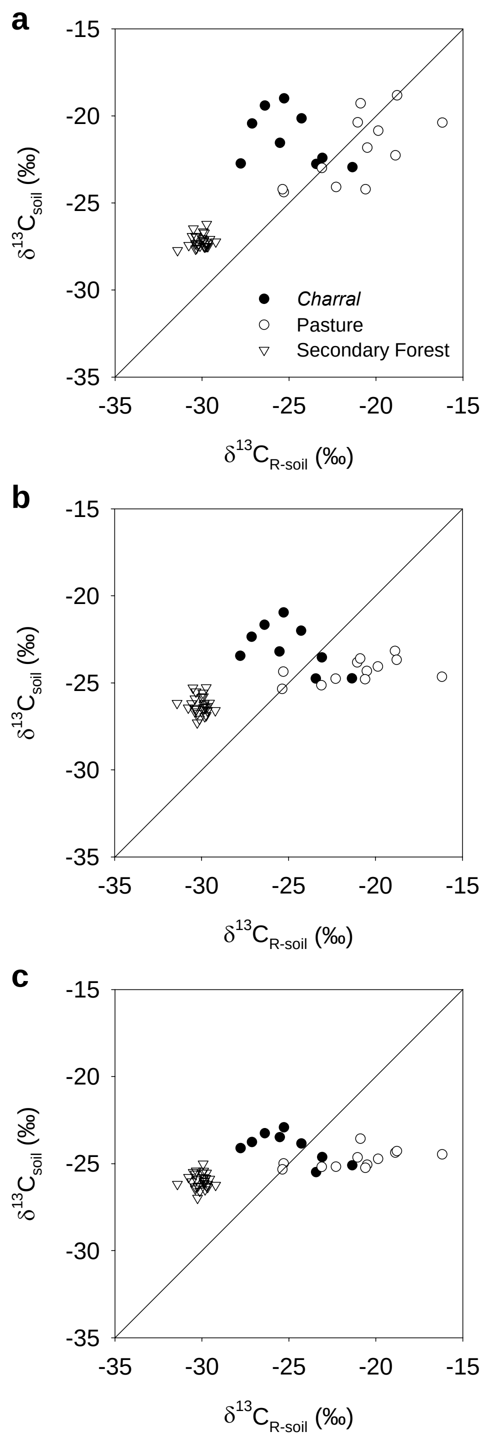

Figure 5. Mean mineral soil $\delta^{13}C$ ($\delta^{13}C_{soil}$) at depths of (a) 0-10, (b) 10-20, and (c) 20-30 cm vs. mean $\delta^{13}C$ of soil respired CO_2 ($\delta^{13}C_{R\text{-}soil}$) for all pasture (○), *charral* (●), and secondary forest (▽) sites. The diagonal line through each plot is the 1:1 line.

CHAPTER 4. CONSEQUENCES OF ENVIRONMENTAL SERVICE PAYMENTS FOR FOREST RETENTION AND RECRUITMENT IN A COSTA RICAN BIOLOGICAL CORRIDOR

Abstract

Compensation to landowners for forest-derived environmental services has gained international recognition as a mechanism to combat forest loss and fragmentation. This approach is widely promoted with little evidence demonstrating its prospects for encouraging forest stewardship and conservation. Costa Rica provides a compelling case study where a 1996 Forestry Law initiated environmental service payments and prohibited forest conversion to other land uses. We examined these novel policies to determine their influence on landowner decisions that affect forest change, carbon services, and connectivity in a 2,400 km^2 biological corridor. Landsat images were used to compare landcover changes before and after 1996, and these data were linked to landowner surveys investigating land use decisions. Carbon services provided by secondary forests were examined both above- and belowground. Forest change observations were corroborated by landowner survey data, indicating that environmental service payments contributed positively to forest retention and recruitment following implementation of the 1996 Forestry Law. Rates of natural forest loss declined from -1.43 to -0.20 % yr^{-1}. Forest cover and connectivity increased through tree plantations and secondary forest recruitment, but these forest types sometimes replaced natural forest prior to 1996. Secondary forest carbon storage approached values found in primary forest after 25-30 years of succession, though few landowners retained natural regeneration. Secondary forests and attendant carbon services will persist as minor landscape components without legal or financial incentives. The Costa Rican experience provides evidence that environmental service payments can be effective in retaining natural forest and recruiting tree cover when focused in biological corridors.

Introduction

Forest loss and fragmentation represent a global threat to biodiversity, ecosystem processes, and human welfare (Millennium Ecosystem Assessment 2005). Demands on forests and the environmental services they provide are projected to increase as development pressures reduce remaining private forests lacking protected status (Defries and others 2005). In response to these threats, incentive programs encouraging private forest stewardship have emerged, offering compensation to landowners who retain forests and associated services that might otherwise be lost to alternative land uses (Pagiola and others 2002). Direct payments to landowners to plant or protect forests are promoted as an effective mechanism for providing environmental services (Ferraro and Kiss 2002), consistent with the 1997 Kyoto Protocol and the 1992 Convention on Biological Diversity. However, the effects of these payments on forest cover and targeted environmental services remain relatively unknown.

Costa Rica presents a compelling case study to analyze an environmental service payment program (*pago por servicios ambientales*, PSA) that provides direct payments to landowners for reforestation, sustainable forest management, and natural forest protection. Reforestation incentives for private landowners to establish tree plantations were first initiated in Costa Rica following several decades of high deforestation (Watson and others 1998). During the mid-1980s, tradable bonds (CAF) and upfront payments (CAFA) became available to cover costs associated with establishing and maintaining tree plantations (Watson and others 1998). Additional incentives initiated in 1990 targeted sustainable forest management (CAFMA) and were expanded in 1995 to include forest protection. Costa Rica built on the legacy of these programs with the 1996 Forestry Law (no. 7575) that implemented four novel features including: 1) a national definition of forest, 2) prohibition of natural forest conversion to any other land use, 3) deregulation of tree plantation management, and 4) a voluntary PSA program to compensate landowners for watershed protection, biodiversity conservation, carbon sequestration, and aesthetic values.

Legal and institutional support for the PSA program is provided by the National Fund for Forest Financing (FONAFIFO), an organization designed to promote sustainable rural development among small and medium-sized landowners (Snider and others 2003). National PSA priorities have concentrated efforts in biological corridors and poorly developed regions of the country with more than US\$124 million expended on >5000 km^2 of land (FONAFIFO 2006). PSA contracts with landowners typically last for five years and payments range from ~\$220 ha^{-1} for the forest protection program to \$560 ha^{-1} for reforestation.

The objectives of 1996 Forestry Law and PSA are to provide environmental services through forest stewardship; however their impacts on carbon storage, forest structure, and connectivity in fragmented landscapes are unclear. Further, the relative influence of forest policies and programs on landowner decisions to maintain or increase forest cover remains poorly understood. Accordingly, we applied an integrated research approach to determine the extent to which the 1996 Forestry Law and PSA incentives for landowners to maintain or replant forests translate into enhanced forest conservation, carbon services, and connectivity. We studied these processes in the San Juan ─ La Selva Biological Corridor, a PSA focal area designed to retain linkages between protected areas in Costa Rica and southern Nicaragua (Figure 1).

Studies of landcover change detection, ecosystem ecology, and rural sociology were unified to address five specific questions: 1) Has the annual rate of forest loss declined substantially for private forest land in the Corridor as expected under the 1996 Forestry Law? 2) To what extent are changes in forest cover attributable to the ban on forest clearing and/or payments to protect forests? 3) Have incentives for reforestation been a major catalyst for landowners to establish tree plantations? 4) What is the outlook for recruiting forest cover via secondary succession as a potential source of valued carbon services under the 1996 Forestry Law? 5) Are PSA programs an effective conservation mechanism for retaining habitat connectivity between protected areas?

Study Area

The present case study focuses on the San Juan – La Selva Biological Corridor (2,425 km^2) in northern Costa Rica where PSA contracts occur on ~22% (538 km^2) of the land area (Rojas and Chaverría 2005). A larger surrounding study area (6,349 km^2) was selected to facilitate forest land change comparisons in areas bordering the Corridor (Figure 1). The Corridor contains one of the largest aggregations of remnant forest in the region, and private forests outside of protected areas represent an important connection between formerly continuous montane and lowland forests (Butterfield 1994a). Diverse vegetation types in the Corridor cross five Holdridge Life Zones and three transitional zones given the region’s varied climatic conditions along altitudinal and longitudinal gradients (Holdridge 1967).

Costa Rica passed its first Forestry Law in 1969 (no. 4465) that has since undergone several revisions. However, agricultural development and colonization programs have taken precedent over forest stewardship, leading to forest cover reductions in the country’s northern region since c. 1950 (Butterfield 1994b). Colonization programs expanded roads and settlements during the 1970s to open territory to landless farmers (Butterfield 1994b), while low interest loans for cattle production and high beef prices further enhanced land colonization and conversion of forest to pasture (Schelhas 1996). Forests were used as an open access resource by colonists, contributing to rapid deforestation and highly fragmented landscape conditions (Butterfield 1994a).

A severe economic crisis at the end of the 1970s forced Costa Rica to accept monetary assistance (Montanye and others 2000) tied to a series of structural adjustment loans that led to the promotion of non-traditional export crops (e.g. pineapple, heart of palm) (De Camino and others 2000). Cattle exports dropped significantly in the early 1980s and cattle herd sizes declined after 1988 (Ibrahim and others 2000). This trend reduced pressure to clear natural forest and led to temporary abandonment of some pastures. However, many pastures were soon converted to crops or used for government land redistribution programs (Butterfield 1994b). Costa Rica continued the promotion of export crops simultaneous with conservation initiatives throughout the 1990s. Evolving development strategies continue to raise questions about how forests will fare under new policies.

Methods

Several data integration efforts were used to address the research questions above. We compared forest retention, recruitment, and other landcover changes derived from satellite images before and after 1996 with landowner surveys to evaluate the influence of forest policy and PSA incentives on observed forest patterns. We also examined secondary forest carbon storage using plot-level data linked to landcover changes and landowner decisions regarding secondary forest establishment. Finally, we employed forest connectivity metrics as a unifying measure of forest retention and recruitment within the Corridor.

Forest and landcover change

We selected five Landsat Thematic Mapper (TM) satellite images (WRS Path 15 Row 53) with low cloud cover from years 1986, 1996/97, and 2001 to observe landcover changes before and after implementation of the 1996 Forest Law. For simplicity, we refer to the time period before the 1996 law (1986-1996) as T1 and the period afterward (1996-2001) as T2. ENVI v.4.1 image processing software (RSI 2004) was used to prepare and classify images. All images were individually co-registered to a 1996 TM image referenced to locations on the ground for spatially accurate comparisons.

Forest and landcover categories were selected based on prior landcover information for northern Costa Rica from 1996 (Pedroni 2003). Five forest categories were used for landcover change detection analyses including: 1) natural forest (closed canopy or selectively logged old-growth forest and natural palm swamps), 2) a *charral* phase (native shrub and herbaceous regeneration), 3) secondary forest (native tree-dominated regrowth up to 15-20 years old), 4) tree plantations (mainly traditional single species exotic or native reforestation), and 5) gallery forest (forest retained along watercourses comprised of remnant trees and forest regrowth). Additionally, we identified two agricultural land use categories: 6) pastures and 7) annual or perennial crops (e.g. pineapple, sugarcane, bananas, heart of palm).

A supervised image classification was implemented using the Rulegen extension in ENVI v. 4.1 and the Quick, Unbiased, Efficient, Statistical Tree algorithm by Loh and Shih (1996). Elevation, topographic moisture index, percent slope derived from a 90 m digital elevation model (DEM), and the Normalized Difference Vegetation Index (NDVI) were used in addition to TM bands 1-5 and 7 to enhance discrimination of forest and landcover types. Training sites for each category were selected from aerial photos, forest inventory maps, and ground reference points collected in the field between 2004 and 2005. The spatial grain of each landcover category was set at a 1 ha minimum mapping unit for comparisons between image dates.

A classification accuracy evaluation for landcover data obtained an average of 94% overall accuracy with a difference of ±3% between dates and an average kappa score 0.93 scaled at -1 to 1 for all image dates (cf. Congalton and Green 1999). Forest categories showed an acceptable degree of accuracy that averaged from 71% for gallery forests to 95% for natural forests. Landscape complexity increased with time generating lower, but acceptable class accuracy above 80% in later image dates for all classes but gallery forests.

We used area summaries for landcover categories from each image date to compare the larger case study area and the Corridor where PSA programs are focused. Differences in rates of change in forest categories were used to compare forest retention and recovery in T1 and T2 within the Corridor. An annual rate of change for each period and forest category was estimated using a standardized rate formula by Puyravaud (2003),

$$r = (1/t_2 - t_1)) \times \ln(A_2/A_1)$$

where A_1 is the forest area at the first time interval (t_1) and A_2 is the forest area at the second time interval (t_2). Additionally, Wilcoxon Signed Rank tests compared the size distribution of patches ≥1 ha in size converted from a forest type to another land use category across T1 and T2. The FRAGSTATS spatial statistics package (v. 3.3 build 5; McGarigal and others 2002) calculated patch cohesion, percentage of like adjacencies, and mean Euclidean nearest neighbor metrics as indicators of connectivity, aggregation, and isolation for the Corridor. We compared fragmentation indices across the three image dates at the landscape level and for each forest type.

Landowner decision making

To help explain landcover changes in T1 and T2 and identify whether forest policies and PSA incentives positively influenced landowner decisions to retain natural forest and participate in reforestation programs, we conducted a livelihoods analysis examining household decisions in the context of national and international economic markets and policies (Geist and Lambin 2001; DFID 2003). A household survey instrument was used to collect data about historical on-farm tree management including natural forest, *charral*, secondary forest, tree plantations, and gallery forest. The survey measured the five livelihood assets (social, human, financial, physical, and natural) and explored the influence of the 1996 Forestry Law and PSA on land use decisions, motivations to enroll land in PSA programs, production options, and future plans for forest currently enlisted in PSA. As PSA is a voluntary program, participants and non-participants were compared across livelihood assets to identify variables likely to influence participation.

We used a FONOFIFO database of all PSA participants (n=510) to randomly select a sample of 99 households within the Corridor. Those receiving reforestation incentives from previous programs (e.g. CAF, CAFA) were included as participants because their payment contracts were continued under the 1996 Forestry Law. A sample of 108 non-participants was selected from the Ministry of Agriculture's 2000 Costa Rican Cattle Census and paired spatially with those in the participant sample. Sample sizes provided a sampling error of ±10% (Salant and Dillman 1994) with only 6 refusals. The unit of analysis was the household, and a research team administered questionnaires via face-to-face survey interviews averaging one hour per household.

Summary data were developed from specific questions regarding on-farm tree management and motivations to participate in PSA programs. A decision tree analysis was used to compare the livelihood assets of incentive program participants and non-participants.

Decision-tree thresholds provide the break point values used to identify boundary levels of assets where incentives may induce landowner participation in a PSA program. Participants with forest protection and management contracts were analyzed separately from those with reforestation because ownership of ≥2 ha of forest land is required by the former two PSA options.

Above- and belowground carbon storage in secondary forests

We selected a chronosequence of twelve secondary forest sites developing on former pasture to examine secondary forest development and the potential of these forests to provide environmental services via carbon storage. Secondary forest development as a mode of forest recruitment was probed in landowner surveys, and the selected study sites represent *charral*, secondary forest, and pasture landcover types identified in the land change detection. Sites included: 1) three young sites in the *charral* phase of development, characterized primarily by shrubs and herbaceous cover, 2) nine older secondary forest sites eligible for legal classification as forest by 1996 Forestry Law standards, and 3) four active pastures grazed for at least 18 years. Fifteen sites were located on acidic, highly weathered Ultisols derived from volcanic parent material, and the remaining site was located on an Inceptisol derived from alluvial deposits.

At each site, soil samples were collected from four locations in each of three plots at depths of 0-10, 10-20, and 20-30 cm. Three samples per depth were composited for percent soil carbon determination, and the fourth sample was used for bulk density determination. We derived soil carbon content at the Idaho Stable Isotopes Laboratory, and data are reported on a volume basis.

Within the nine secondary forest sites, three 50×50 m plots were established to determine species and diameter at breast height (1.37 m, dbh) for all trees, palms, and lianas ≥5 cm dbh. When present, dbh measurements were made above buttresses. Data were used to estimate total aboveground biomass using the equation for wet forest stands by Chave and others (2005) that accounts for differences in wood density among species. Estimates of aboveground biomass were multiplied by 0.5 to determine aboveground carbon storage. Remnant trees comprised of stems ≥60 cm dbh (<1% of all stems at these sites) were removed from the dataset.

For soil carbon analyses, we employed the statistical language R (v. 2.0.1, R Development Core Team 2004). Mean soil carbon storage was analyzed separately by depth class, and linear mixed-effects models (Pinheiro and Bates 2000) were used to examine changes across land use types. Significant differences detected with analysis of variance (ANOVA) were further examined via multiple comparisons procedures.

Results and Discussion

Patterns of natural forest retention

Notable differences in the status of natural forest occurred between the larger study area and Corridor over a relatively short time period (15 yrs). Land change estimates showed a striking decrease in the annual rate of natural forest loss from -1.43% yr^{-1} in T1 to -0.20% yr^{-1} during T2 inside the Corridor (Table 1). Natural forest loss in T2 occurred primarily outside the Corridor in areas that became an increasingly heterogeneous mixture of pasture, crops, and tree plantations (Fig. 2a; b). This pattern indicates that areas outside the Corridor remained vulnerable to forest loss regardless of the 1996 Forestry Law's forest change restrictions. Reduced forest loss in the Corridor, where a high density of forest protection and management contracts were established during T2, was concurrent with implementation of the 1996 Forestry Law and PSA. High rates of forest loss during T1 were consistent with other forest change studies conducted in the region (Read and others 2001; Sánchez-Azofeifa and others 2003). Significantly larger natural forest patches were converted to other land uses in T1 relative to T2 ($p < 0.001$). Large contiguous forest patches (>150 ha) were removed prior to 1996 (67 in T1 vs. 5 in T2), creating highly fragmented forest conditions in the northeastern portion of the Corridor (Figure 3).

Data from landowner surveys showed that 65% of the total sample population owned natural forest and 59% of these individuals received payments for protection. Forty-four percent of landowners receiving PSA did not intend to clear or harvest any forest. However, 33% of respondents with PSA indicated that they would convert some of their forest to pasture or crops, while 19% would harvest some timber in the absence of PSA and the Forestry Law's legal restrictions on forest land use change. Therefore, PSA payments provided protection against forest clearing and harvesting. This is in contrast to findings from landowners interviews on Costa Rica's Osa Peninsula where PSA was found to have little to no immediate impact on forest protection (Sierra and Russman 2006).

A landowner's dependence upon his or her farm as a primary source of income constituted the principal livelihood variable differentiating PSA participants from non-participants in the forest protection and management programs ($p < 0.0001$). Participants had a lesser dependence on their farms for income than non-participants, suggesting that individuals whose livelihoods depended less directly on farm income were more likely to participate in PSA. Our observations confirm similar patterns found in this and other regions of Costa Rica (Miranda and others 2003; Zbinden and Lee 2005). However, the PSA program for forest protection effectively competed with other opportunity costs of forest land, in that it was common for landowners with up to 73% of their income derived from the farm to participate in PSA. Production options for private forest remain limited to timber extraction because of the 1996 Forestry Law's ban on forest clearing. Permits to harvest are limited, so those unable to obtain permits have an opportunity cost of foregone production near zero, and thus, can only gain by entering into a PSA contract. Pagiola and others (2002) noted an excess national demand for the PSA protection program, implying that the same amount of forest protection could likely be provided at lower payment rates (Rojas and Aylward 2003).

Forest recruitment: reforestation

Results from landcover comparisons show that forest cover increased over both time periods with positive consequences for environmental services, primarily during T2. A net gain in forest cover of 0.5% yr^{-1} occurred in T1 and 0.6% yr^{-1} in T2 (Table 1), although gains after 1996 were concurrent with greatly reduced natural forest loss. In general, land withdrawn from forest cover may constitute a loss of environmental services such as biodiversity and carbon sequestration (Snider and others 2003). Increased forest cover in the Corridor for both time periods was mainly the result of a large increase in tree plantations (Figure 2a) established in pastures. Tree plantations increased from 19 km^2 in 1986 to 268 km^2, representing 11% of the total land area in 2001 (Figure 3). These figures compared favorably to the cumulative total of ~380 km^2 reported to have been planted regionally up to 2001 (COSEFORMA 1995; Méndez 2003).

The rate of tree plantation establishment decreased from 24 to 4.6% yr^{-1} during T1 and T2, respectively (Table 1), with significantly smaller pastures planted after 1996 ($p < 0.05$). A number of tree plantations were either harvested or overtaken by natural regeneration by

2001 (data not shown). Although we detected substantial increases in forest cover under plantations, regional figures show that on an area basis, PSA for forest protection (51%) and management (33%) were favored over reforestation programs (17%) (Méndez 2003). These statistics reflect national priorities to reduce forest loss via PSA for forest protection (Snider and others 2003) rather than promote forest recruitment through reforestation. Because forest plantation conversion to other land uses is permitted, their long-term contribution to forest cover and environmental services in this landscape is uncertain.

The trends described above indicate that reforestation incentives fueled a rapid expansion of tree plantations in the Corridor since 1986. Nearly one third of all landowners interviewed (31%) maintained tree plantations on their farms, and the majority (60%) were established through PSA reforestation contracts. Primary motivations for plantation establishment included perceived value of the wood (40%), meeting conservation objectives such as biodiversity protection (20%), and availability of payments (17%). Most reforested land was converted from pasture (88%) while 12% was formerly crop land. Fifty-three percent of landowners indicated satisfaction with the level of PSA payments, with remaining landowners indicating that payments did not meet expected costs. Of those with PSA, a majority (68%) would not have reforested without payments to cover establishment and maintenance costs, demonstrating the importance of financial incentives to induce landowner participation in reforestation activities.

Of those with reforestation under the PSA program, a majority (59%) intended to plant another crop of trees after harvesting their current plantation while a quarter (24%) indicated they would not replant, and 17% remained undecided until final harvests. Landowners reforesting without PSA incentives showed similar patterns. The majority of landowners have adopted forest plantations as a viable economic activity, competitive with other land use options and economic opportunities.

Reforestation incentives were a critical factor in forest cover gained from tree plantations during T1 and T2. A landowner's dependence on his or her farm as a primary source of income was the primary livelihood variable differentiating PSA reforestation participants from non-participants ($p < 0.0001$). However, a division between groups occurred at the point where 16% of the household income was derived from the farm, with individuals more likely to participate below this point. Results show that PSA for reforestation remains uncommon for landowners moderately dependent upon their farms as a source of income, indicating that payment rates are not adequate to motivate most farm-dependent individuals to forgo current production systems.

Forest recruitment: secondary vegetation and gallery forest

Successional vegetation occupied between 8 and 10% of the Corridor area at any one point in time, maintaining persistent areas of natural regeneration in the Corridor (Figure 3). However, the total land area in the early successional *charral* phase declined during the study period from 9% in 1986 to 4% in 2001 (Figure 2a), indicating that the outlook for recruiting new secondary forest stands was lower after 1996. Although land area in secondary forest increased slightly after 1996, the patch size of both secondary forest and *charral* areas recruited significantly declined ($p < 0.001$). Additions to the area occupied by secondary forest (Table 1) during T2 accounted for some of the losses in the *charral* phase as succession proceeded.

Our landcover data show that forest recruitment via secondary succession may represent only temporary gains in connectivity and short-lived opportunities for habitat restoration. An overall decline in land area occupied by *charral* (Table 1) indicates that landowners abandoned very little pasture land throughout the study period, as observed previously by Read and others (2001). The low level of secondary forest establishment in the Corridor did not follow patterns of agricultural abandonment conducive to forest recruitment encountered elsewhere in Costa Rica (Arroyo-Mora and others 2005). The amount of pasture land allowed to recover to the *charral* stage was offset by a greater amount being returned to pasture in both T1 and T2. This observation is corroborated by data from landowner surveys indicating that only 13% of respondents had *charral* on their property. Of these individuals, 56% maintained *charral* for economic reasons, while 20% cited conservation reasons. The role of economics in decisions to maintain *charral* shows that natural forest regeneration in the Corridor was likely limited by PSA incentives for reforestation, agricultural export opportunities, and restrictions in the 1996 Forestry Law prohibiting land use change.

Survey data supports the observation that much of the land converted to *charral* (68%) or secondary forest during our study period previously existed as pasture (Figure 2; 4). Although *charral* and secondary forest occupy a small amount of land area relative to natural forest, these forest types are ecologically important as sites for forest recruitment, carbon sequestration, and habitat restoration (Holl and Kapelle 1999). *Charral* typically persists on abandoned land for a short period of time before a tree canopy develops, but restrictions on forest clearing provide incentives for landowners to inhibit the development of secondary forest (Sierra and Russman 2006). Surveyed landowners planned to clear 43% of existing *charral* for pasture or agricultural use in the future, thus limiting the potential for carbon storage (Murty and others 2002).

Transitions from pasture to secondary forest reveal differences in carbon storage at shallow soil depths. Pastures contained a greater amount of mineral soil carbon at 0-10 cm relative to *charral* and secondary forest, but there was high variability within land use classes (Table 3). Mineral soil carbon storage in pastures rapidly decreased with depth, and both *charral* and secondary forests had significantly higher soil carbon storage than did pastures at depths of 10-30 cm (Table 3). High levels of soil carbon storage in *charral* at 10-30 cm depth likely occurs from shifts in rooting depth and subsequent alteration of organic carbon inputs to the soil at an early successional phase (Jackson and others 1996; Jobbágy and Jackson 2000). A decline in soil carbon storage at these depths in secondary forest relative to *charral* was not unexpected, as these sites were dominated by more deeply rooted trees.

Managed crops remain a competitive land use with secondary forest on former pasture (Figure 4), and agricultural transitions can decrease soil carbon stores up to 30% during the first decades of cultivation (Murty and others 2002). Survey respondents also suggested reforestation as another common land use option on former pasture land (Figure 4), and although plantations often increase soil carbon storage in the tropics (Silver and others 2000), this is not always the case (Powers 2004). In relation to competing land uses, secondary forests may provide considerable carbon services.

Above- and belowground carbon storage rapidly increased toward values observed in primary forest following secondary forest establishment. For 0-30 cm, soil carbon storage in secondary forests was slightly lower (70.9 Mg C ha^{-1}) than the regional mean of 82.2 Mg C ha^{-1} in primary forests (Powers and Schlesinger 2002). Aboveground, secondary forest stands appear to pass through a period of low biomass accumulation and reach the point of stem exclusion after 20 to 25 years of development (Figure 5). Following this phase, 25 to 30 year old secondary forests had aboveground carbon stocks equivalent to those in primary forests of the region (Figure 5; Clark and Clark 2000). The carbon services provided by secondary forest rival those of natural forest and merit greater attention from forest management and policy perspectives. Our data show that forest policies and incentives have effectively influenced land-use decisions for tree plantations, and similar incentives for natural regeneration could enhance carbon storage as a targeted PSA environmental service.

In addition to carbon storage, benefits accruing from secondary forest recovery include forest structural connectivity, natural habitat development, and new timber resources (Finegan 1992; Lamb and others 1997). Secondary forests provide a number of potential economic and restoration opportunities that contribute positively to the goals of the San Juan-La Selva Biological Corridor. The existence of competing land uses with greater financial returns than secondary forest suggests that financial incentives and technical support may be necessary to secure the environmental services provided by these forests. The recent introduction of PSA for natural regeneration (FONAFIFO 2006) represents significant progress in acknowledging the benefits of secondary forest, though the program remains confined to western Costa Rica.

Gallery forests also have important consequences for recruiting forest cover in the Corridor, increasing from 2 to 6% of the total land area during T1 and T2, respectively (Table 1). Linear forest arrangements of remnant trees and secondary vegetation were retained along waterways as surrounding forests were cleared in T1. We interpreted an increase in post-1996 gallery forests as forest recruitment because few large patches of natural forest were removed in T2. Forest land along perennial rivers and streams has received protection by laws designed to conserve water resources since 1942. Eighty-five percent of landowners sampled in the Corridor had land occupied by gallery forest. Recruitment patterns in T2 reflect a social commitment to protecting water resources as 87% of survey respondents gave conservation-oriented reasons for retaining tree cover in riparian areas.

Forest and landscape connectivity

We analyzed the spatial and temporal arrangement of forests in the Corridor as an indicator of physical connectivity among protected and privately owned forests. Connectivity varied across T1 and T2 for total forest cover (landscape indices) and individual forest types (class indices). Landscape indices in the Corridor showed a decline in connectivity and aggregation among all forest patches during T1, and a maintenance of conditions with some enhanced connectivity during T2 (Table 2). These patterns reflected the higher rate of natural forest loss observed in T1 relative to T2 (Table 2), but can be partially explained by the development of increasingly heterogeneous forest conditions. At the class level, natural forests comprised the majority of total forest cover and became increasingly distant from one another over time, reflected by increased isolation and decreased aggregation (Table 2). In contrast, patterns in reforestation, forest regrowth, and gallery forest showed trends with an overall positive impact on forest connectivity and aggregation (Table 2). Patches of reforestation and secondary forest regrowth tended to aggregate in a few areas of the Corridor (Figure 3).

Greater natural forest retention in T2 and recruitment throughout the study period indicates that the 1996 Forest Law and prior reforestation programs contributed to a net increase in forest connectivity. Landowner decisions to participate in PSA programs have increasingly affected the process of reconnecting forests in this landscape. Though monocultures of fast growing exotic species occupy many of the reforested areas, a recent shift toward native tree species has occurred. Native species plantations have the potential to support diverse understory flora (Cusack and Montagnini 2004) and attract wildlife (Lamb and others 1997), but the overriding homogeneity of tree plantations may detract from natural forest connectivity. During T1 some tree plantations with low species and structural diversity replaced natural forests following short-term use as pasture. After this land use change became illegal in T2, significantly fewer natural forest patches were converted to tree plantations ($\Delta T1 > \Delta T2$, $p < 0.001$).

Secondary forests play a role in maintaining forest structural connectivity, often developing on land adjacent to natural forest (Figure 3). The benefits of secondary forest cover on the landscape in terms of forest connectivity, biodiversity value, and carbon services may outweigh those of tree plantations in light of 1996 Forestry Law objectives. As secondary vegetation reaches a successional stage with at least 60 tree stems >15 cm dbh ha^{-1}, it is legally classified as forest and can no longer be cleared for alternate land uses. Because plantations are harvested on short rotations and can be legally converted to non-forest uses, retention of new forest cover through secondary succession is more likely to be a permanent type of forest cover. However, secondary forests are likely to have a less positive economic impact on local livelihoods when compared to plantations.

Many of Costa Rica’s recognized corridor areas resemble stepping stones of forest habitat within agriculturally-dominated landscapes because intensively managed crops typically support little or no tree cover. The implications of the 1996 Forestry Law in conjunction with the data reported here reflect on an emerging importance of forest recruitment via a variety of pathways. As natural forests were replaced by reforestation and secondary forests, a fundamental change in forest structural connectivity occurred. This highlights the need to examine the functional role of these new forest connections where forest cover is best characterized as a mosaic of habitats with variable economic and ecological potential.

Conclusions

Costa Rica’s innovative strategies to maintain private forest land and environmental services showed notable progress toward these goals in the Corridor. The rate of natural forest loss was substantially less after 1996 relative to the previous time period. Legal restrictions in the 1996 Forest Law forbidding land use change reduced the opportunity cost of forest land, influencing landowners moderately dependent on their farms for income to participate in the PSA forest protection program. Continued high rates of natural forest loss outside the Corridor after 1996 indicated that restrictions on forest clearing without the benefit of PSA were not sufficient to induce forest retention in this region.

PSA directly influenced landowner decisions to substantially increase forest recruitment during the study period. Specifically, reforestation incentives prior to PSA led to a dramatic increase in plantation forests during T1, while a slower increase occurred following PSA implementation in T2. Forest recruitment via secondary forest development occupied a relatively constant amount of land area in the Corridor through time. However, disincentives for secondary forest development existed in the form of lost land use opportunities once an area returned to forest. Carbon services provided by 25-30 year old secondary forests were similar to those in primary forest, suggesting that these forests deserve greater attention from a land management perspective.

Positive outcomes of the 1996 Forestry Law were further illustrated by changes in forest cover dynamics that enhanced forest structural connectivity in the Corridor in T2, relative to T1. In the future, adaptations of the PSA program such as that recently implemented for natural regeneration in western Costa Rica will continue to provide flexibility in tailoring the program to diverse and changing landscapes. As a case study, the Costa Rican experience with PSA provides evidence that environmental service payment programs in conjunction with legal forest protection are effective in retaining natural forest and recruiting new forest cover when focused in the Corridor as a priority conservation area. PSA has been tailored to fit Costa Rica's socioeconomic conditions, but shows promise as an effective conservation approach with prospects for adaptation to other settings.

Acknowledgements

This research was supported in part by NSF-IGERT grant no. 0114304. Thanks for assistance is due to Edwin Pereira, Marvin Zamora, Vicente Herra, José Manuel Ulate, Sandra Candela, Isabel Venegas, Zayra Ramos, Hugo Brenes, Germán Obando, Andrés Sanchún, Pablo Acuna, Oscar Quirós, Jhonny Méndez, Nelson Zamora, Robin Chazdon, and Juan Pablo Arroyo. We are also indebted to the organizations FUNDECOR and CODEFORSA, as well as numerous landowners in the study area.

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Table 1. Forest change for T1 and T2 by forest type. The amount of forest lost or gained during each time period was estimated by subtracting the total area for each forest category in the Corridor from the previous year's land cover data ($\Delta T1$=1986-96, $\Delta T2$=1996-01). The annual rates of forest cover change by type and net forest gain before and after 1996 were estimated using the formula by Puyravaud (2003) and expressed as percentages. Net forest cover includes all five forest types.

Forest cover type	**$\Delta T1$ (km^2)**	**$\Delta T1$ yr^{-1} (%)**	**$\Delta T2$ (km^2)**	**$\Delta T2$ yr^{-1} (%)**
Natural forest	-179	-1.43	-12	-0.2
Reforestation	194	24.15	55	4.57
Charral	-42	-2.25	-60	-8.93
Secondary forest	69	18.95	20	4.31
Gallery forest	36	5.21	48	8.66
Net forest cover	78	0.47	50	0.58

Table 2. Fragmentation indices for the Corridor landscape and individual forest classes indicating changes in physical connectivity at each landcover date. The level of isolation was determined using Euclidean nearest neighbor distance (ENN) to measure isolation, patch cohesion (PC) as an indicator for physical connectivity among like patches, and percentage of like adjacencies (PLA) as a measure of aggregation of similar patches.

	Isolation: ENN (m)			**Connectivity: PC (%)**			**Aggregation: PLA (%)**		
Category	**1986**	**1996**	**2001**	**1986**	**1996**	**2001**	**1986**	**1996**	**2001**
Landscape	256.2	241.8	249	99.3	99	98.9	89.8	88.1	88.3
Natural forest	130.6	135.4	142.7	99.76	99.68	99.68	94.83	94.02	93.91
Reforestation	337	202.3	187.9	86.59	97.06	97.91	71.34	81.81	81.36
Charral	164.3	191.1	250.9	93.28	93.33	93.82	74.14	75.2	77.28
Secondary forest	526.4	215.7	227.9	83.46	89.09	92.68	67.39	70.48	74.05
Gallery forest	238.5	216.9	188.1	87.57	89.2	92.19	67.66	71.78	74.57

Table 3. Mean mineral soil carbon storage ± one standard error across all land use types and soil depths. Reported *p*-values were derived from individual ANOVAs performed for each soil depth. Superscripted letters represent the result of means separation performed using pre-planned contrasts in the Multcomp package of R. Different superscripted letters represent significant differences among categories.

Soil depth	**Pasture soil carbon (Mg ha^{-1})**	***Charral* soil carbon (Mg ha^{-1})**	**Secondary forest soil carbon (Mg ha^{-1})**	***p*-value**
0-10 cm	43.69 ± 3.09^{a}	34.65 ± 2.31^{b}	35.70 ± 1.13^{b}	0.012
10-20 cm	18.71 ± 1.38^{a}	25.00 ± 1.63^{b}	20.65 ± 0.69^{c}	0.0048
20-30 cm	12.60 ± 0.65^{a}	17.53 ± 1.63^{b}	14.57 ± 0.73^{c}	0.0167

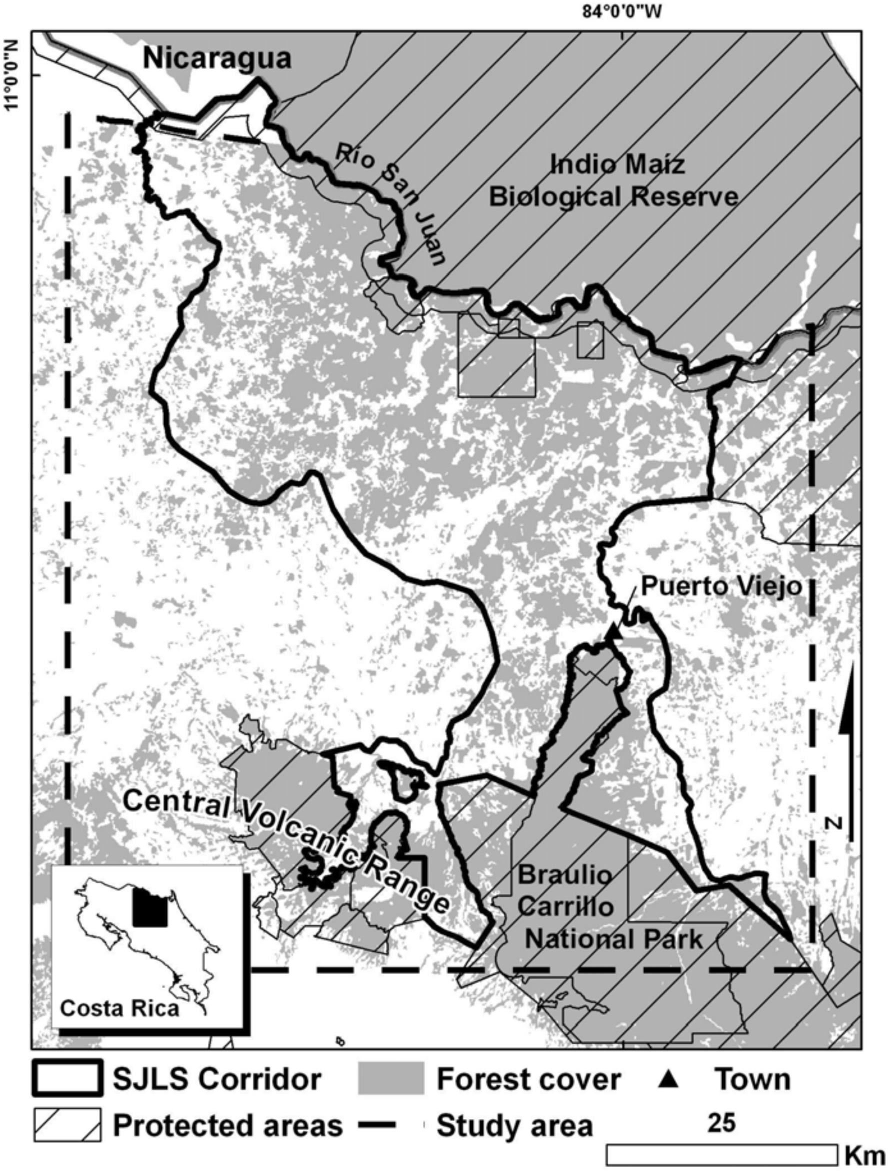

Figure 1. Map of the San Juan – La Selva Biological Corridor, connecting national parks and protected areas, and the larger study area. Depicted natural forest cover is for year 2000 (Atlas of Costa Rica 2004).

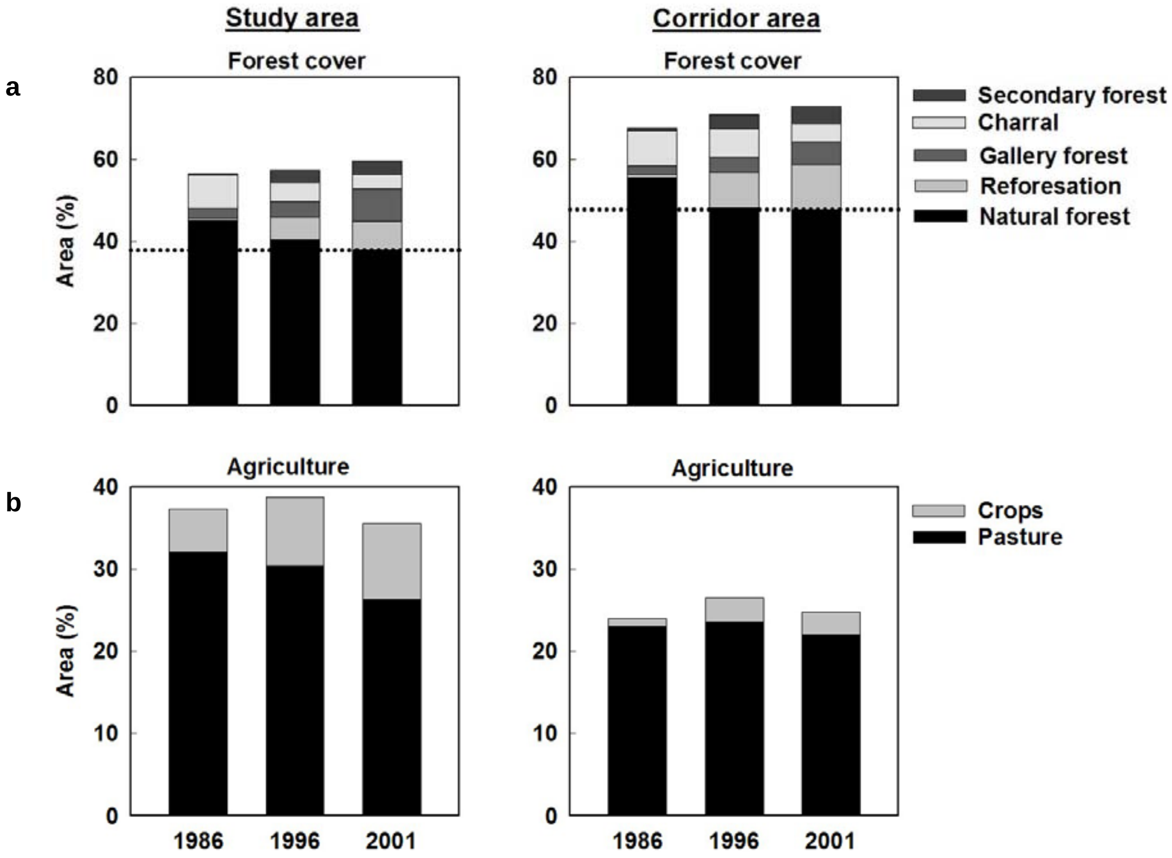

Figure 2. Area differences for each time interval for (a) the five forest categories and (b) two agricultural categories observed at the extent of the study area (6,349 km^2) and the San Juan – La Selva Biological Corridor (2,425 km^2). Dotted lines above the natural forest category show the top of the bar in year 2001, indicating that a greater percentage of natural forest loss occurred outside of the Corridor after 1996.

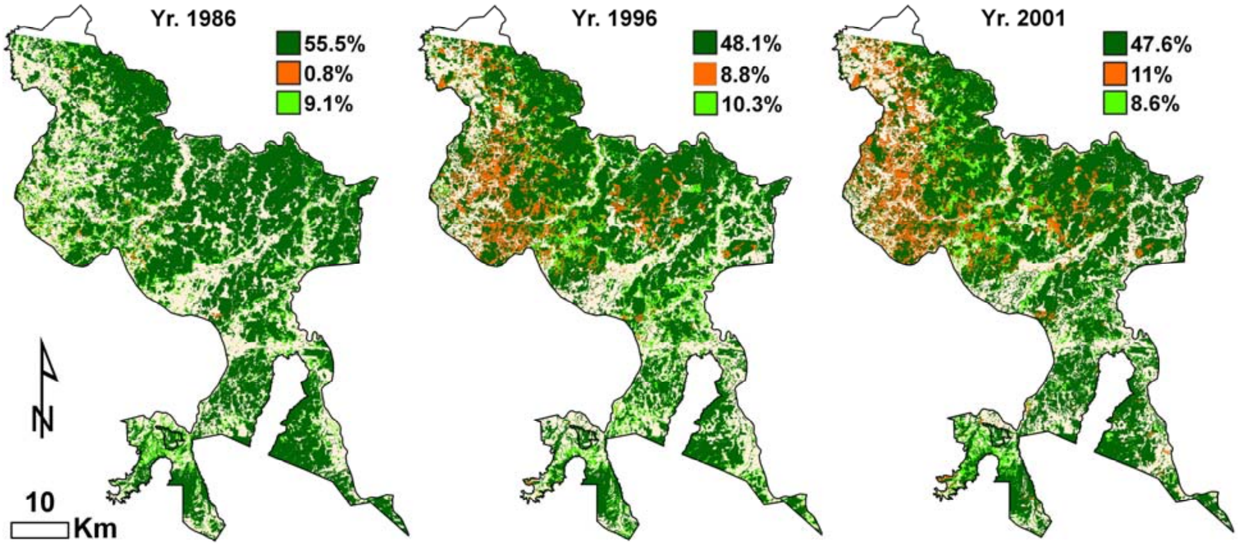

Figure 3. Mapped forest cover in the San Juan – La Selva Biological Corridor depicting major landscape changes at each time interval using the forest categories natural forest (dark green), forest regrowth (*charral* and secondary forest, bright green), and reforestation (orange).

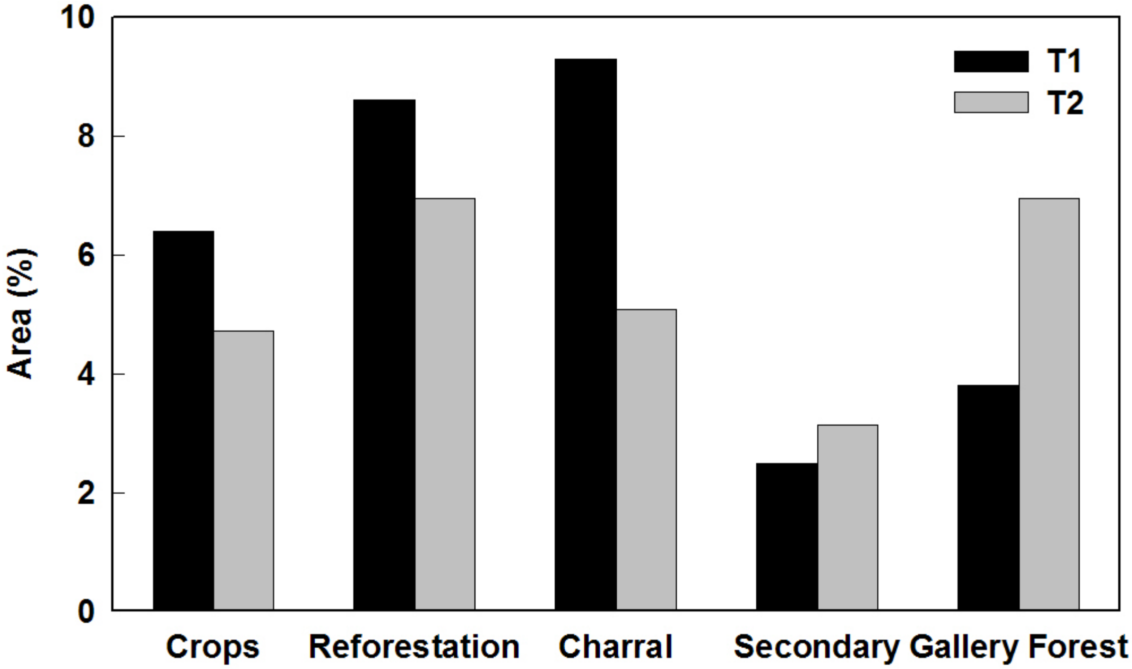

Figure 4. Amount of pasture converted to another forest or landcover type in the San Juan – La Selva Biological Corridor during time periods T1 and T2.

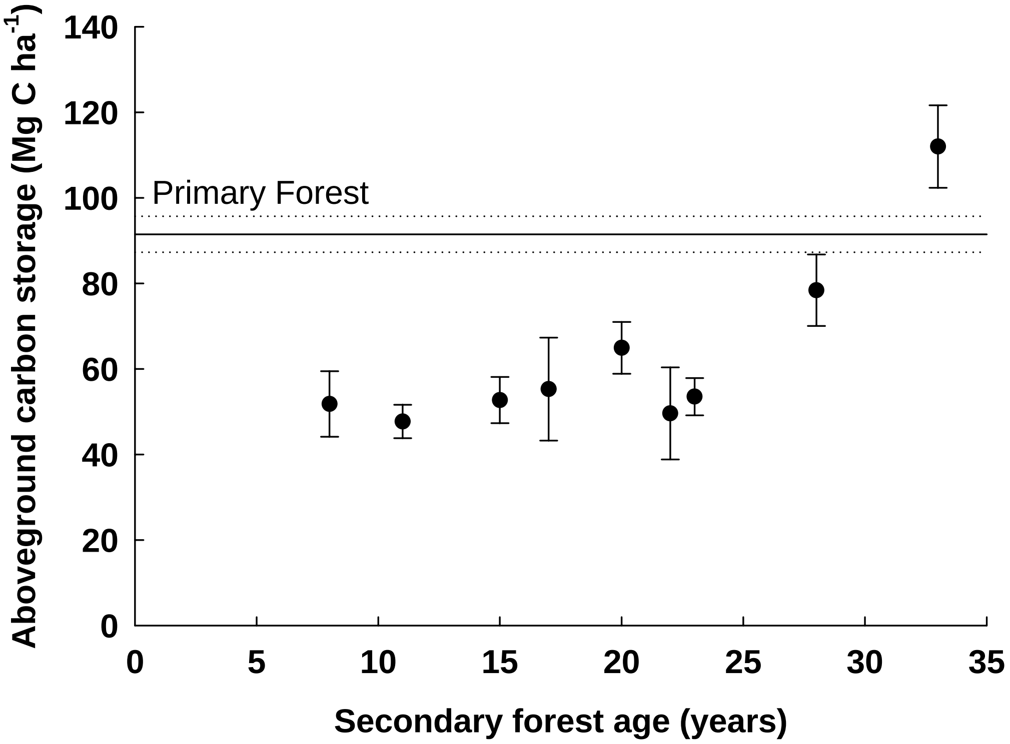

Figure 5. Mean aboveground carbon storage ± one standard error for each secondary forest site. The solid and dotted horizontal lines represent mean aboveground carbon storage and one standard error, respectively, as measured in undisturbed primary forests at the La Selva Biological Station (Clark and Clark 2000). Values were calculated as one half of aboveground biomass estimates for all stems ≥10 cm dbh in plots ≥ 4 ha.