Chapter 2
Trends in Above and Belowground Carbon with Forest Regrowth After Agricultural Abandonment in the Neotropics

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2.1 Introduction

Increasing forest cover on lands which were recently forested (reforestation), as well as on lands which have not supported forest growth in recent times (afforestation), has been proposed by the Intergovernmental Panel on Climate Change (IPCC) to help mitigate anthropogenic C emissions from land-use change and fossil fuel use (Brown et al. 1995a, Watson et al. 2000, Metz et al. 2001). Recent research has suggested that these strategies would be most effective in the tropical latitudes (Gibbard et al. 2005). Tropical forests have higher potential carbon (C) uptake rates than forests in temperate or boreal biomes (Brown et al. 1995a, Watson et al. 2000). Globally, 40% of terrestrial biomass C is in tropical forests (Dixon et al. 1994), and 40% of this is in secondary forests (Brown and Lugo 1990). In addition to providing opportunities for C sequestration, reforestation can lead to the recovery of important forest ecosystem goods and services. These include, but are not limited to, watershed protection, erosion control, regional climate stabilization, wood and non-timber products, and habitat for biodiversity (Brown and Lugo 1990, Guariguata and Ostertag 2001, Naughton-Treves and Chapman 2002, De Walt et al. 2003).

Although deforestation is still a dominant trend across the tropics, secondary forests resulting from human disturbance are becoming an increasingly important forest cover type (Brown and Lugo 1990). Just as rates of deforestation are difficult to establish with certainty (see Achard et al. 2002, DeFries et al. 2002, Eva et al. 2003, Fearnside and Laurance 2003), estimates for rates of secondary forest growth also differ, although most agree that the trend is positive. In the 1980s, tropical secondary forests were estimated to cover more than 600 million hectares (ha) globally with an annual rate of formation of 9 million hectares per year (ha/yr), and growing (Brown and Lugo 1990). In 1993, the estimated area of tropical America covered by secondary forests was 165 million ha (Weaver 1995 in Kammesheidt 2002). The United Nations Food and Agriculture Organization in 1990 classified 33 million ha of previously agricultural or pasture lands in Latin America as fallow (cited in Kammesheidt 2002). These fallow lands are key components of forest regrowth

R. W. Myster, *Post-Agricultural Succession in the Neotropics.*

and succession toward secondary forest cover. In many regions across the tropics, reforestation is in the form of agroforestry systems or plantations. Reforestation also occurs due to natural regeneration of forest species on abandoned cropfields or pastures, or by active planting and management which facilitate the process of secondary succession.

The factors behind the increase in secondary forest growth in the tropics vary by region, as do the initial drivers of deforestation, but typically include one of the following: shifts in economic bases from agriculture to industry, rural to urban migration across domestic and international borders, changes in land tenure policies, or loss of site fertility (Rudel et al. 2002, Aide and Grau 2004, Soares-Filho et al. 2004, Arroyo-Mora et al. 2005). Brown and Lugo (1990) identified regional differences in the former land use type prior to secondary forest growth. In tropical America and Africa, most secondary forests originated from agricultural fallows. In tropical Asia, logging was a more important contributor to secondary forest formation than agricultural abandonment. Tropical Africa had the smallest percentage of secondary forests from logging. The authors also documented differences in the disturbance history of the pre-conversion forest leading to secondary forests. At the time of their review, 58% of secondary forests in tropical America were first generation secondary forests, from previously undisturbed or primary forest. In contrast, 72–76% of secondary forest areas in tropical Africa and Asia had experienced multiple cycles of disturbance (Brown and Lugo 1990). However, regional trends can change as economic policies are altered, and an updated study considering current trends in globalization and its effect on reforestation would be a valuable undertaking.

In this chapter, we review the recent literature on the effects of reforestation on above and belowground C stocks in both natural and managed secondary forests and plantations growing on former agricultural and pasturelands. We revisit Silver et al.'s (2000a) analysis of the potential for C sequestration with reforestation in the tropics with new data published since their review. We limit our analysis to studies from the Neotropics, where the bulk of studies are still located, though we would like to point out that in recent years there has been an increase in publications on biomass and structural changes during secondary forest and plantation development in the African and Asian tropics (e.g., de Jong et al. 2001, Lemenih et al. 2004, Walker and Desanker 2004, Lawrence 2005a, Makana and Thomas 2006). We also highlight advances made in the study of soil C dynamics with land-use change, particularly, and provide suggestions for future research directions.

2.2 Reforestation in the Neotropics

Changes in economic policies and human migration have resulted in agricultural abandonment and reforestation across the tropics. A prime example of the increase in secondary forest cover during the last half-century is the Caribbean island of Puerto Rico, where the most reliable data on secondary forest cover exists, along with Costa Rica and the Brazilian Amazon (Kammesheidt 2002). Economic changes in Puerto Rico, beginning in the late 1940s with the transition from being a colonial dependency to a free associated state (Dietz 1986), resulted in a large-scale abandonment of agricultural and pasturelands at an approximate rate of 10,000 ha/yr from 1950 to 1990 (Grau et al. 2004). These abandoned lands generally reverted to secondary forests through natural succession (Marrero 1950, Weaver and Birdsey 1990). As a consequence, the area of Puerto Rico under forest cover, which in the mid-1940s was only 13%, increased to 30% by 1980 (Weaver and Birdsey 1990). A similar trend related to forest regeneration on degraded pastures has occurred in the moist lowlands of central and eastern Colombia (Etter et al. 2005). In the Brazilian Amazon, secondary forest area is estimated to have increased five-fold from 2,900,000 in 1978 to 16,100,000 ha in 2002 (Neeff et al. 2006). For example, one municipality (Igarapé) in Pará, Brazil reached 73% secondary forest cover by the late 1990s (Neeff et al. 2006). While often this increase in secondary forest cover represents a net gain in total forest cover with the loss of agricultural and other cleared lands, in many areas, such as the Brazilian Amazon, an increase in secondary forest cover is directly related to the loss of mature or primary forest.

An increase in secondary forest cover on formerly cleared lands for agriculture or pasture typically represents an increase in forest biomass and associated C stocks. Regional C fluxes are often estimated as gains or losses of C stocks at the landscape scale (Houghton et al. 1991, Fearnside and Guimarães 1996). Carbon gain or release at the landscape scale is estimated as the change in carbon content due to changes in biomass of the vegetative cover. Aerial and satellite-based remote sensing technologies have been used for estimating forest successional class, biomass, and geographical extent in Costa Rica (Helmer et al. 2000) and the Brazilian Amazon (e.g., Houghton et al. 2000, Neeff et al. 2006). Determination of the net carbon balance of tropical forests requires certainty in biomass estimates of the different land cover types, accurate estimates of the spatial extent at a landscape scale and on the rates of conversion, and ways to extrapolate from plot-level studies to regional scales (Powers et al. 2004). Secondary forest biomass, and hence their C stocks, are affected by a suite of environmental and ecological factors which are discussed in this chapter.

2.3 Tropical Forest Carbon Stocks and Their Measurement

The carbon budget of a tropical forest is affected by the balance of C inputs (primary production) and C outputs (respiration, decomposition, erosion, leaching losses), and can be expressed by a simple donor-controlled model:

$$\frac{\partial C}{\partial t} = \text{Inputs} - kC$$

where $\partial C/\partial \mathrm{t}$ is the rate of change in C content over time and kC represents the output term, where C is the standing stock of carbon and k is a decay constant. In non-steady state systems, C accumulates when the rate of inputs into a particular pool exceeds outputs and/or the rate of outputs decreases, either by a reduction in the standing stock or a decrease in turnover time ($1/k$). Attempts to increase C storage in an ecosystem will often involve the transfer of C into pools with longer turnover times, which increases the amount of time a C molecule is not in the atmosphere where it can act as a greenhouse gas. The potential for tropical forests to remove C from the atmosphere and store it effectively depends on net primary productivity and the residence time of C in each reservoir. An actively growing forest functions as a C sink as trees increase in height and diameter, and the amount of C fixed is greater than C lost in respiration and in decomposition of litterfall. Carbon uptake by plants can be defined as the net annual removal of C from the atmosphere per unit of land area, which can measured by a change in biomass over time (Fearnside 1996).

A forest in C balance, or steady-state, may also store C if the residence time of C in the largest stocks is long. The largest and longest-lived C reservoirs in tropical forests are soil organic matter and standing live aboveground biomass (tree boles). Tropical soils can contain more than twice as much C as in aboveground biomass (Post et al. 1982) and have the potential to store C at great depths (Nepstad et al. 1994, Jobbágy and Jackson 2000). The residence time of C in tropical soils varies greatly with soil depth and soil type. In the highly weathered Oxisols and Ultisols, mean residence time of bulk soil C in the top 10 cm is on the order of decades (Trumbore 1993, de Camargo et al. 1999, Amundson 2001), while residence times of up to 20,000 years have been reported for mineral horizons at depth in some volcanic soils in Hawaii (Torn et al. 1997). Substantial C stocks can be stored in large trees (> 80 cm in diameter) which may live up to 1,000 years (Chambers et al. 1998), though 300–500 years may be more representative of an average lifetime for large canopy and emergent trees (Fichtler et al. 2003).

A common method for studying the successional regeneration and temporal C dynamics of secondary forest on abandoned lands is the use of chronosequences. Using this method, forest stands of different ages are selected, using age as a proxy for successional time. An important assumption of this method is that the patterns observed across the chronosequence will be comparable to the patterns occurring at one site over time. Another common method is paired-site comparisons, where secondary forest sites or plantations are compared to primary forests, typically in close proximity. In this chapter we include data from both chronosequence and paired site studies.

2.3.1 Aboveground Carbon Stocks

Carbon stocks in vegetation are generally calculated as 50% of dry biomass; or 45% for young secondary forests due to the presence of a larger proportion of early succession trees with lower wood density than in mature forests (Fearnside and Guimarães 1996, Alves et al. 1997). Plant biomass can be measured directly by harvesting and weighing all components in a specified area, or calculated from allometric equations using measured parameters such as diameter-at-breast-height, wood volume, and stem height. The advantages and uncertainties associated with different methods of measuring secondary tropical forest and plantation biomass have been evaluated in detail elsewhere (e.g., Brown and Lugo 1984, Brown et al.

1989, 1995b, Chambers et al. 2001, Keller et al. 2001, Losi et al. 2003, Brandeis and Suárez Rozo 2005). Significant stores of C can also be found in root biomass (Nepstad et al. 1994), in standing and fallen coarse woody debris (Delaney et al. 1998, Clark et al. 2002, Keller et al. 2004, Rice et al. 2004) and in lianas, particularly in disturbed forests (Gerwing and Farias 2000, Read and Lawrence 2003a).

2.3.2 Belowground Carbon Stocks

Carbon in soils exists in organic forms: soil organic matter (SOM) and dissolved organic carbon (DOC), or in inorganic forms: carbonates, with a minor proportion as CO_2 gas in soil pores or dissolved as carbonic acid in soil water. Most highly weathered tropical soils are acidic, and so the major component of soil C is organic. In the drier tropics or in young soils derived from limestone, karstic soils can contain significant amounts of inorganic C (Crowther 1980). In this chapter we discuss changes in organic C pools, which are the focus of the majority of tropical studies on highly weathered soils. Changes in C storage are affected by changes in the rate of organic C inputs (e.g., above- and belowground litter, dissolved organic C) and outputs (e.g., C mineralization, leaching losses, erosion). The residence time of C in soils is regulated by a variety of physical, biological, and chemical mechanisms, which affect microbial decomposition and losses of C by other means (reviewed in Paul 1984, Oades 1988, Sollins et al. 1996, Krull et al. 2003, Mikutta et al. 2006).

Soil organic matter (SOM) is a heterogeneous mixture of plant, animal and microbial residues in different stages of decomposition (Stevenson 1982, Kögel-Knabner 1993). In addition to acting as one of the largest terrestrial reservoirs of C (Post et al. 1982, Eswaran et al. 1993), SOM is an important contributor to soil fertility as a source of plant nutrients and through its enhancing effects on soil structure, its high water holding capacity, and buffering capacity (Tiessen et al. 1994). SOM also provides energy and nutrients for microbial metabolism (Lovley et al. 1996, Scow 1997) and plays an important role in metal contaminant and pesticide binding due to its high sorptive capacity (Balabane et al. 1999, Ahmad et al. 2001, Farenhorst 2006). SOM concentrations were traditionally measured by wet oxidation (Walkley and Black 1934). More commonly used today are the loss of ignition method for SOM (Dean 1974), where the amount of C is calculated as 50% of the SOM mass, and by gas chromatography, which is a much faster, automated method (Byers et al. 1978, Nelson and Sommers 1996). The C content of a particular soil profile is then calculated by multiplying % C by the bulk density of the soil sampled and by the depth of the soil core and summed over the total depth in question (Veldkamp 1994).

2.4 Trends in Carbon Stocks with Reforestation: Data Analysis

We surveyed the recent literature and updated secondary forest biomass and soil C data presented in Silver et al.‘s (2000a) review. In that review, data of above and belowground C accumulation from secondary forests across the tropics was analyzed with respect to time by prior land use abandonment, prior land use type, and annual rainfall. We extracted their data from studies in Neotropical sites and added about 90 data points to their aboveground biomass and more than 100 data points to their soil C database from new studies published since their review. The abundance of studies on C dynamics with reforestation being published in the last 7 years testifies to the importance this topic has gained.

Data for this chapter were collected from chronosequence and paired site studies. We included forests and plantations growing on former croplands and pastures resulting from unassisted as well as assisted, unmanaged and actively managed regeneration. We tested for the effect of previous land use (agriculture, pasture or cleared), present cover type (secondary forest versus plantation), and life zone. For consistency, we followed the site classification used by Silver et al. (2000a): life zones were based on annual precipitation, and included dry (<1,000 mm/yr), moist (1,000–2,500 mm/yr), and wet (>2,500 mm/yr). While a lot more studies have been published since Silver et al.'s (2000a) review, some of the same methodological constraints persist. For example, data are still very strongly skewed towards the first two decades of regrowth and to the wet and moist life zones. In addition, aboveground biomass estimates in individual studies are likely influenced by the authors' choice of allometric equation and plot size (for discussion of uncertainties surrounding tropical forest biomass measurement and estimation, see Brown et al. 1995b, Alves et al. 1997, Chambers et al. 2001, Keller et al. 2001, Brandeis and Suárez Rozo 2005).

To identify trends in aboveground C accumulation, we ran regressions on C by life zone, past land use and cover type (planted versus secondary succession) over time since abandonment. We use site age and time since abandonment interchangeably. To avoid the effect of uneven representation of past land uses across biomes and vice versa in our dataset, we also tested the effect of land use within moist forests only, which had the highest representation of all land uses (59 agricultural sites, 21 cleared, 19 pasture), and the effect of life zone on agricultural lands only, which had the highest representation of all life zones (17 wet forests, 59 moist, 28 dry). To fulfill assumptions of normality, we used the natural log of aboveground C and site age. All secondary forest and plantation ages were used, but we did not include mature or primary forests in our regressions with time as we are uncertain of their real age.

To examine patterns in soil C with reforestation, we compiled data from studies that reported either soil C content (on a per area basis) or both soil C concentrations (on a per soil mass basis) and bulk density values. SOM values were converted to C by multiplying by 0.5. Our more recent literature search increased the range of soil depths reported (from 0.05 to 8.0 m) from the Silver et al. (2000a) review, although most studies still sampled in the top 0.50 and 0.25 m. Following Silver et al.'s (2000a, 2000b) technique, we used regressions to determine soil C relationships with depth to standardize all studies to a common depth of 0.25 m. The wet and dry life zone equations were derived from the literature dataset. Soil C in the wet life zone decreased with depth according to the linear equation $y = 1.29 + 0.84x$ ($r^2 = 0.66$, $p < 0.0001$, n = 98) where y= log C and x = log depth. For the dry forests, the relationship was $y = 2.34 + 0.59x$ ($r^2 = 0.86$, $p < 0.005$, n = 7).

The literature dataset gave a weak relationship ($r^2 = 0.28$) for the moist forests, so we used an equation derived from detailed soil C profiles sampled every 10 cm to 1.0 m depth in 18 moist forests in Puerto Rico, $y = 2.36 + 0.52x$ ($r^2 = 0.66$, $p < 0.0001$, n = 180) (Marín-Spiotta, unpublished data). These sites included primary forests and secondary forests aged 10, 20, 30, 60 and 80 years and so the equation incorporates age variability such as that found in our larger database. We used these equations to calculate multipliers for the maximum depth or the depth closest to 0.25 m, whichever was smallest reported, for each site to adjust soil C stocks to the standardized depth. We report soil C data for forests older than 3 years.

All statistical analyses were conducted on JMP IN version 5.1 software (SAS Institute). We tested for relationships between soil C and forest age (years), life zone (wet, moist, dry), and previous land use (pasture, agricultural crops, cleared and abandoned), and present cover type (plantation, secondary forest). We compared mean soil C stocks between secondary forests, plantations and mature forests used as end-members in the cited studies, and between life-zone using Wilcoxon/Kruskal-Wallis nonparametric test because C stocks were not normally distributed and variances between sample sizes were unequal.

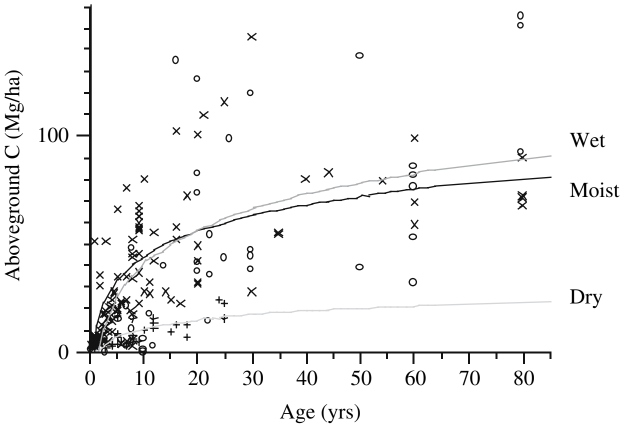
2.4.1 Aboveground Biomass Accumulation: Results and Discussion

Aboveground C accumulation showed significant log-linear trends with time for all life zones and past land uses (Table 2.1, $p<0.0001$). Only planted cover types did not show a significant trend with time. Moist and wet forests had greater rates of C accumulation than dry forests overall. During the first 20 years of succession moist forests accumulated C fastest than wet forests, while wet forests accumulated more total C in the long-term (Fig. 2.1). When comparing forests growing on agricultural

Table 2.1 Best fit regression equations for aboveground carbon (Mg/ha) with time following tropical reforestation. See Appendix 1 for data

Parameter	Equation	r^2	p	n
All data	Aboveground C = −4.0 + 18.6*(ln AGE)	0.44	<0.01	190
Life zone				
Moist forests	Aboveground C = 3.0 + 17.7*(ln AGE)	0.53	<0.01	107
Wet forests	Aboveground C = −15.5 + 24.0*(ln AGE)	0.48	<0.01	47
Dry forests	Aboveground C = −2.9 + 5.9*(ln AGE)	0.48	<0.01	28
Past land use				
Agriculture	Aboveground C = −1.5 + 15.1*(ln AGE)	0.43	<0.01	104
Pasture	Aboveground C = −38.9 + 28.7*(ln AGE)	0.60	<0.01	41
Cleared	Aboveground C = −17.4 + 37.8*(ln AGE)	0.77	<0.01	25
Cover type				
Plantations	n.s.			10
Secondary forests	Aboveground C = −4.3 + 18.6*(ln AGE)	0.44	<0.01	182

Note: n.s., not significant

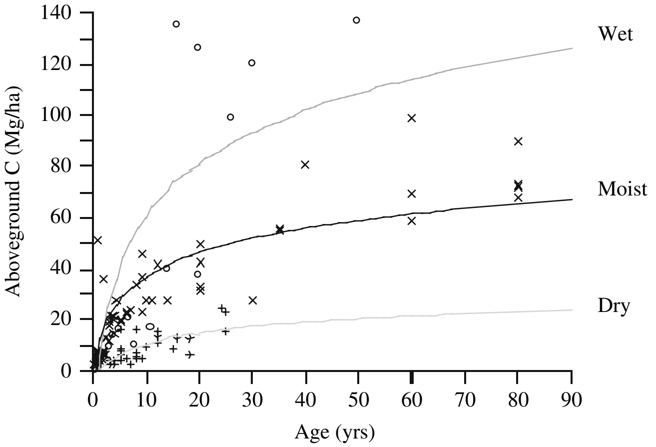


Log curve fits are shown for aboveground C accumulation in secondary tropical forests. + = dry forest, x = moist forest, o = wet forest.

Fig. 2.1 Aboveground carbon accumulation during secondary succession by life zone

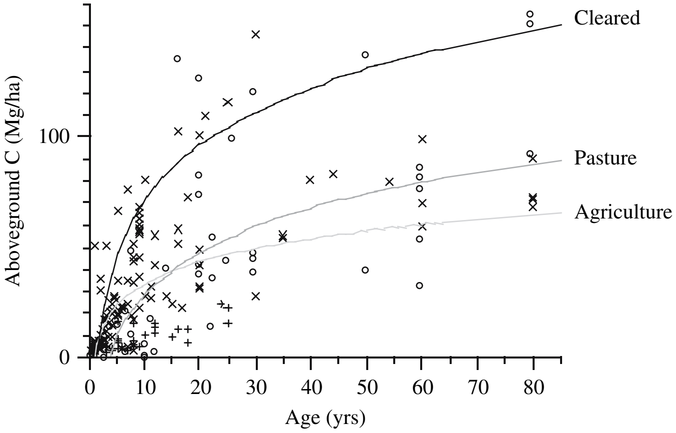
land only to control for the effects of past land use, wet forests clearly had the highest rates of aboveground C accumulation, while dry forests had the lowest (Fig. 2.2).

Among past land uses, cleared lands showed the highest overall rates of aboveground C accumulation during 80 years of succession (Fig. 2.3). During the first 10 years of succession, agricultural land appeared to have had higher rates of aboveground C accumulation than pastures, but over longer succession pastures surpassed agricultural lands (Fig. 2.3). This trend was maintained when analyzing only moist forests, which had the most even representation of all past land uses (data not



Log curve fits are shown for aboveground C accumulation in secondary tropical forests. + = dry forest, x = moist forest, o = wet forest.

Fig. 2.2 Aboveground carbon accumulation by life zone for agricultural lands only



Log curve fits are shown for aboveground C accumulation in secondary tropical forests. + = dry forest, x = moist forest, o = wet forest.

Fig. 2.3 Aboveground carbon accumulation during secondary succession by past land use

shown). In an ANOVA including all factors, time, life zone, past land use and cover type were all significant ($p < 0.05$, $r^2 = 0.55$).

Greater aboveground C accumulation in wet and moist forest life zones than dry ones is consistent with the first two biomes being more productive overall (Brown and Lugo 1982). The differentiation between wet and moist forests was much clearer when examining only agricultural land than when all past land uses were included, showing the importance of past land use for regeneration in these forests. This also implies that wet and moist forests may have similar potentials for aboveground C accumulation during secondary succession depending on the local mosaic of land use history.

Our results comparing previous land uses were more surprising, and were in contrast to Silver et al. (2000a), who found that agricultural land had the highest rates of C accumulation aboveground and that cleared areas had the lowest rates. This difference could be related to a number of new data points added to the study that had secondary succession on land that had been cleared and then allowed to grow back within < 2 years in the Brazilian Amazon (Lucas et al. 2002), and a number of new data points for land regenerating on agricultural land in a dry forest in the Yucatan (Read and Lawrence 2003a). However, our test of past land use in moist forests only showed that the trend for highest regeneration potential on recently cleared land held, with agricultural and pasture land regenerating at slower rates. Many of the cleared forests were allowed to grow back within a short time period (Lucas et al. 2002), while other land uses like agriculture were maintained for over 50 years in some cases (Schroth et al. 2002). This implies that the length of land use prior to abandonment could be as important, or more so, than the type of previous land use for aboveground C accumulation.

2.4.2 Patterns in Soil Carbon with Reforestation: Results and discussion

On average, moist forests had significantly higher soil C stocks to 0.25 m (95.0 ± 6.4 Mg/ha, mean ± 1 standard error, $n = 81$) than wet forests (67.2 ± 2.8 Mg/ha, $n = 100$) and dry forests had intermediate values (67.7 ± 4.03 Mg/ha, $n = 12$). There were no significant differences between forests growing on former agricultural lands (95.7 ± 8.2 MgC/ha, $n = 61$) and those on abandoned pastures (71.9 ± 2.5 MgC/ha, $n = 83$), or between forests $\geq$ 20 years old (86.6 ± 6.6 MgC/ha, $n = 55$) and those > 20 years old (71.9 ± 3.1 MgC/ha, $n = 109$). Across all life-zones, there were no significant differences in soil C between mature forests (90.8 ± 12.7 Mg/ha, $n = 29$), plantations (72.1 ± 6.5 Mg/ha, $n = 31$) and all secondary forests grouped together (80.6 ± 4.9 Mg/ha, $n = 90$).

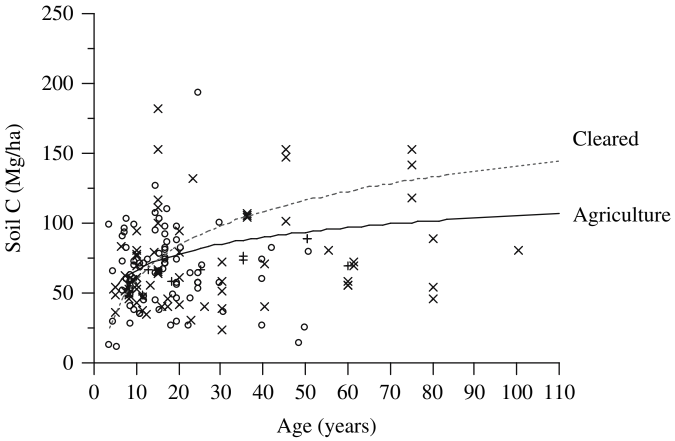
Time since abandonment had a significant ($p < 0.01$) but very weak ($r^2 = 0.05$) effect on soil C stocks to 0.25 m (Table 2.2). The strongest relationship we found between age and soil C was for the dry forests, although this life-zone had the smallest number of data points. Wet forests, which comprised the larger sample size, did not show any significant trend, similar to Silver et al.'s (2000) findings. Past land-use also had a significant effect on soil C, with forests on formerly cleared-only land showing the strongest relationship ($r^2 = 0.41$, $p = 0.06$) while those on former agricultural sites showed a weaker relationship (Table 2.2 and Fig. 2.4). Sites regrowing on former pastures did not show any trend over time since abandonment. With respect to current cover type, both secondary forests and plantations showed significant, but very weak relationships between soil C stocks and site time.

Silver et al. (2000a) reported a slightly more robust relationship ($r^2 = 0.11$, $p < 0.05$) between time and soil C for all ages with a smaller dataset (n = 57) compiled from pantropical studies. While sites with different land use history and across the

Table 2.2 Best fit regression equations for soil carbon (Mg/ha) (in the top 0.25 m) with time following tropical reforestation. See Appendix 2 for data

Parameter	Equation	r^2	p	n
All ages				
All data	SOIL C = 42.8 + 9.3*(ln AGE)	0.05	<0.01	164
Life zone				
Moist forests	SOIL C = 34.9 + 9.3*(ln AGE)	0.09	0.01	70
Wet forests	n.s.			85
Dry forests	SOIL C = 15.0 + 17.0*(ln AGE)	0.64	<0.01	9
Past land use				
Agriculture	SOIL C = 27.1 + 17.2*(ln AGE)	0.12	<0.01	57
Pasture	n.s.			83
Cleared	SOIL C = −23.4 + 35.6*(ln AGE)	0.41	=0.06	9
Cover type				
Plantations	SOIL C = 25.9 + 15.0*(ln AGE)	0.15	<0.05	31
Secondary forests	SOIL C = 38.1 + 10.2*(ln AGE)	0.05	<0.05	90

Note: n.s., not significant



Log curve fits are shown for changes in soil C in secondary tropical forests. Former pastures showed no significant trend. + = dry forest, x = moist forest, o = wet forest.

Fig. 2.4 Soil carbon stocks during secondary succession by past land use

three climatic zones studied accumulated aboveground biomass C during secondary succession, soil C stocks changed very little, or not at all, with time since abandonment. Soils appeared to respond very differently than aboveground biomass and may be more resilient to changes in land use and plant cover. Formerly cleared sites appeared to accumulate soil C faster than agricultural sites, similar to the pattern observed in aboveground biomass. The low predictive power of time suggests that there are other factors influencing rates and direction of soil C changes with secondary succession in the tropics. In the following sections we explore other factors from individual studies that potentially determine the rate and magnitude of soil C change during reforestation.

2.5 Land-Use Change and Tropical Forest Carbon

At a global scale, aboveground biomass and soil C stocks are influenced by climate (precipitation and temperature), soil and vegetation type, and ecosystem age (Schlesinger 1977, Post et al. 1982, Eswaran et al. 1993, Torn et al. 1997, Malhi et al. 1999, Jobbágy and Jackson 2000). Human activities, such as logging and deforestation for agriculture or pasture establishment, mining, dam construction or urban development also affect C storage in forests (Parrotta and Knowles 1999, Caspersen et al. 2000, Houghton and Goodale 2004). The loss of aboveground C during deforestation has been documented extensively (e.g., McWilliam et al. 1993, Fearnside 1996, Houghton et al. 2000, Hughes et al. 2000). After the removal of a disturbance, C stocks may recover or attain a new steady-state below or above pre-disturbance levels. In areas where climate is favorable to forest growth and a seed source is available (Uhl 1987, Holl et al. 2000, Chazdon 2003), natural regeneration of intensively used lands is possible. Many areas of tropical forest which had been previously considered to be untouched primary forest, are instead located on sites of intense human agricultural activity and are in different stages of recovery from disturbance (Bush and Colinvaux 1994, Chazdon 2003).

Multiple environmental, ecological, and anthropogenic factors interact to determine the rate of natural or managed reforestation at any one place, making it difficult to predict the success of reforestation at a particular site, or to estimate regional and global C sequestration potentials of regrowing forests. At the broadest scale, climate affects primary productivity and forest regrowth after a disturbance (Johnson et al. 2000, Anderson et al. 2006). Whether the driving forces behind the initial change in land use and land cover are extrinsic (economic policy) or intrinsic (soil degradation) is likely to affect the regenerative potential of a site. Previous land-use history, the type, intensity, and duration of use, can affect the successional trajectory of a site, and its potential to recover from a disturbance (Nepstad et al. 1991, Aide et al. 2000, Silver et al. 2000). Furthermore, the same factors may have opposite effects on rates of above and belowground C accumulation (Silver et al. 2000). The frequency of a natural or anthropogenic disturbance, such as hurricanes or fire, may also slow down forest regrowth (Zarin et al. 2005).

In the following sections, we discuss recent literature on the factors affecting tree biomass, coarse woody debris, litterfall, roots, and soil C stocks during reforestation in the Neotropics. We refer the readers to Post and Kwon's (2000) review for the potential for C sequestration after agricultural abandonment in soils under natural or replanted perennial vegetation (forests and grasslands) across different global climatic zones. More recent reviews by Pregitzer and Euskirchen (2004) and Anderson et al. (2006) explore ecosystem C and biomass C changes with forest age globally by biome, although they do not distinguish between the type of disturbance before succession.

2.6 Trends in Aboveground Carbon

2.6.1 Tree Biomass

2.6.1.1 Natural Regeneration

The success and rate of secondary forest regeneration depends on a multitude of factors, including prior land use, climate, available seed source, and soil fertility. While early secondary succession can be fast, with biomass accumulations estimated up to 25–50 t/ha on 5-year-old sites, and up to 75–150 t/ha on 15-yr-old sites throughout the Amazon basin (Neeff 2005), subsequent recovery may be slower, and can depend on species composition and forest type (Gehring et al. 2005). Typically, forest regeneration on former croplands and pastures results in net C sequestration aboveground due to greater C stocks in longer-lived trees with the accumulation of woody biomass. In Silver et al. (2000a), prior land use had a significant effect on aboveground biomass accumulation, with C accumulation on abandoned agricultural fields > abandoned pastures > previously cleared sites. Compared to other land uses, grazing can lead to greater soil compaction (Spiel 1996) and slower recovery of forest height and basal area (Aide et al. 1995, Zimmerman et al. 1995, Stern et al. 2002, Chazdon 2003). In agricultural fields, different crops can have "signatures," such as root exudates, associated species, and effects of fertilizers and herbicides, all of which can influence soil properties and affect subsequent succession (Myster 2004). The distinction between prior land-uses is sometimes confused because conversion of forest first to agriculture and then to pasture once soils become nutrient depleted is common across tropical forests (Buschbacher 1986, Uhl et al. 1988, Fearnside 1993, Thomlinson et al. 1996, Carpenter et al. 2001). In some areas, like the Brazilian Amazon and in Colombia, direct conversion to cattle pasture was more common in the last 40 years (Fearnside and Guimarães 1996, Etter et al. 2005), but today, soybean cultivation is one of the main drivers of deforestation (Hecht 2005, Nepstad et al. 2006, Steward 2007). Other factors affecting regeneration include disturbance history, landscape mosaic, and physical environment (Lugo 1988, Murphy and Lugo 1995, Marcano-Vega et al. 2002).

Land use history also has an effect on C storage through its influence on successional trajectories in secondary Neotropical forests. Although successional forests may recover structural characteristics in as little as 20–30 years (Guariguata and Ostertag 2001, Kennard 2002), species composition may remain distinct in old secondary forests (Zou et al. 1995, Aide et al. 2000, Lugo and Helmer 2004, Marín-Spiotta et al. 2007). In a study of secondary dry tropical forests, Read and Lawrence (2003a) related aboveground biomass to forest age, while forest structure was most affected by water availability and anthropogenic disturbances. After a disturbance, different regeneration pathways could affect biomass accumulation (Uhl et al. 1981, Lucas et al. 2002). In a wet secondary forest chronosequence on abandoned pastures in Puerto Rico, 80-year old secondary forests had greater aboveground biomass than primary forests because of the dominance of woody species in the former, and a heavy dominance of palms in primary forests (Marín-Spiotta et al. 2007). Shifts in life-form and an increase in the abundance of palms in the seedling community with secondary succession have been described in wet tropical forests in Costa Rica (Capers et al. 2005), which may affect aboveground structure and biomass as the forests age. A comparison of species composition scenarios for a forest on Barro Colorado Island, Panama, by Bunker et al. (2005) found that future aboveground C storage could vary by several hundred percent, depending on species composition. Thus, which species predominate during secondary succession may have a large influence on the future C storage of these lands. A chronosequence study in the Brazilian Amazon showed that a history of slash and burn agricultural had a large effect on forest structural characteristics, affecting the full recovery of aboveground biomass (Gehring et al. 2005). Use of fire and mechanization during clearing have been shown to slow down recovery of biomass (Uhl et al. 1981, 1988, Zarin et al. 2005). The legacy of land-use history can persist through a natural disturbances such as hurricanes (Boucher et al. 2000, Pascarella et al. 2004).

Forest growth generally occurs at different rates during early versus later stages of succession. Early phases of succession are generally observed to be the times of greatest C accumulation in aboveground biomass, as observed in high-altitude tropical forests of Ecuador (Fehse et al. 2002a), and stem density has been seen to peak at intermediate age classes in moist tropical forests (Saldarriaga et al. 1988, Mizrahi et al. 1997, Denslow and Guzmán 2000, Kennard 2002, Ruiz et al. 2005,). Silver et al. (2000a) found that overall aboveground biomass had significantly faster biomass accumulation during the first 20 years of succession (6.17 Mg ha^{-1} yr^{-1}) than the subsequent 60 years. Nonetheless, tropical forests generally show relatively fast aboveground growth, up to 70% of mature forest height and basal area can be reached in 25 years, as observed on prior agricultural lands in moist forests of the Bolivian Amazon (Peña-Claros 2003) and dry Bolivian forests (Kennard 2002). Rapid early growth during secondary succession can lead to 50% recovery of aboveground biomass in a variety of biomes, from moist (Gehring et al. 2005) to dry (Read and Lawrence 2003a), though Read and Lawrence (2003a) estimated that mature-forest levels of biomass could take over 100 years to reach in dry forests in the Yucatan because of slower growth at later stages of succession. However, many secondary forests are much younger than 25 years, and may never reach maturity before they are cleared again, with great implications for long-term C sequestration. Neeff et al. (2006) estimated that the average age of secondary forests in the Brazilian Amazon in 2002 was 5 years.

Soil fertility can be an important factor affecting forest regeneration. Tropical soils are typically old, highly weathered Ultisols and Oxisols that are poor in mineral-derived nutrients such as phosphorous, calcium, and other base cations (Brady and Weil 2002). Prior land uses such as repeated fire and long-term pasture use may also lead to losses of nitrogen from soils. In a fertilization experiment on abandoned pastures in the Brazilian Amazon, Davidson et al. (2004) found that both grasses and early successional trees during early succession (6 years) responded positively to nutrients, especially nitrogen. Another study in the Brazilian Amazon (Gehring et al. 1999) also found a positive response of vegetation in secondary succession to nutrient additions, but in this case phosphorous was the main limiting nutrient. Gehring et al. (1999) found that different woody species had varying biomass responses to fertilization, but that grasses had the best response and gained a competitive advantage with increased nutrients. Similarly, Uhl (1987) found that nutrient additions favored only grasses on abandoned pastures in Venezuela. In all cases, it is clear that soil nutrient availability can affect both the trajectory of succession and the amount of biomass accrual.

2.6.1.2 Plantations

Planting native and exotic timber species on abandoned pastures is a popular approach for reforestation across the Neotropics. Because of C sequestered in plantations, the proven success of prior large-scale plantations, and a developed professional forestry sector, Latin America has been identified as a potentially key player in global C trading (Wright et al. 2000). Planting woody species can greatly increase the rates of aboveground C accumulation relative to natural succession, especially in areas where herbaceous species such as grasses and ferns can dominate unmanaged succession on abandoned pastures (Aide et al. 1995, Cusack and Montagnini 2004, Myster 2004). Herbaceous species have much lower aboveground C accumulation than woody species (Aide et al. 1995). Planted woody species can improve physical conditions, shading out herbaceous species (Holl 1998, 1999), reducing soil temperatures, and increasing soil nutrient and physical properties, increasing recruitment of other woody species in the understory and promoting forest succession (Oliver and Larson 1996). Prior land use and extent of pasture use can have a strong impact on subsequent C and biomass accumulation in plantations as well, similar to issues discussed above for natural succession (Silver et al. 2004).

There has been extensive study of how the species selected for planting affect forest regeneration and C accumulation. Different species have different growth patterns, making rates of aboveground C accumulation highly variable across plantation types. Aboveground C accumulation can range from as little as 0.8 to as much as 15 Mg C ha^{-1} yr^{-1} during the first two decades of plantation establishment (Lugo et al. 1988). The species planted also have a strong effect on later composition of the stand, with planted timber species an important component of forest species diversity 60 years after planting (Silver et al. 2004). Both native and exotic species have been used to plant abandoned pastures. One advantage of some exotics is that they are fast growing and rapidly accumulate C. For example, a 20-year old teak plantation (exotic species) in Panama averaged 120 Mg/ha in aboveground C (Kraenzel et al. 2003). Due to the importance of planted species in the composition of the forest, there has been an emphasis on planting native species in monoculture and mixed stands. A study of 12 and 13-yr old native species timber plantations in Costa Rican lowland forests found that most species had greater C accumulation in mixed stands than in single species stands. Across three experimental blocks with combinations of 9 native species, mixed stands (64 ± 13 Mg C/ha) had greater C accumulation after 12+ years than pure stands (50 ± 9 Mg C/ha) ($p = 0.1$) (Redondo-Brenes and Montagnini 2006). In this study, plantations with fast-growing species accumulated more C in early stages of plantation development (<10 years), while plantations with slower-growing species were projected to store more C in the long-term. Similarly, mixed species plantations in Hawai'i with Eucalyptus and Albizia (an N-fixer) had greater biomass accumulation after 17 years than monocultures of either species (Kaye et al. 2000). Since species are planted, successional patterns and rates of aboveground biomass accumulation can differ from natural secondary regeneration. Silver et al. (2004) found that timber trees grew fastest during the second 33 years than the first 22 years, indicating that C accumulation is important during later stages of succession. This contrasts with findings for natural succession, as discussed above.

2.6.2 *Litterfall*

Despite a considerable amount of work on changes in vegetation structure during tropical secondary forest development using chronosequences, where sites vary in time since forest regrowth, most studies of litterfall do not use this approach (but see Lawrence 2005b). More commonly, studies compare secondary forest of a single age to plantations or to primary forest (e.g., Cuevas et al. 1991, Lugo 1992, Li et al. 2005), or compile data worldwide across forests of different ages (e.g., Brown and Lugo 1990). Our understanding of litterfall nutrient inputs to the forest floor and soil during tropical secondary succession seres is therefore limited.

Secondary forests are generally categorized as establishing high rates of litterfall relatively quickly, within the first 25 years of succession (Ramakrishnan and Toky 1983, Brown and Lugo 1990, Guariguata and Ostertag 2001, Lawrence 2005b), and soon after plateau to a production rate of a primary forest (Ewel 1976). Moreover, litterfall mass is likely to reflect development of biomass during succession (Ewel 1976), with young forests generally having high rates of litterfall in the first 20 years after abandonment (Brown and Lugo 1990, Guariguata and Ostertag 2001). For some recent litterfall studies, see McDonald and Healey 2000, Sánchez-de León and Zou 2004, Silver et al. 2004, Li et al. 2005. Typical values for Neotropical secondary forests range from 6–10 Mg ha/yr, but there is wide variation depending on forest type, age, and climate. Avenues for further study might be developing synthetic models to address how these environmental variables affect litter mass and nutrients, seasonal patterns (Read and Lawrence 2003b), and more long-term studies that directly follow a given site or chronosequences over time. Litterfall has also been shown to influence forest tree seedling and sapling mortality in mature forests (Clark and Clark 1991, Guariguata 1998, Drake and Pratt 2001, Gillman et al. 2004), and its effects on secondary forest community structure would be worth investigating.

2.6.3 *Coarse Woody Debris*

Very little work has been done on fine and coarse woody debris inputs, stocks, or decomposition during tropical succession. Unfortunately, not all studies standardize the diameter ranges of coarse and fine woody debris, but the term usually includes both standing dead and fallen debris (Harmon and Sexton 1996). During secondary succession, coarse woody debris should be accumulating, but initially may be quite low as decomposition rates and slow inputs may initially diminish stocks after land clearing, and thus has been described as a U-shaped curve (Janisch and Harmon 2002). It has been suggested that coarse woody debris does not accumulate in an ecosystem until trees are at least 10 cm diameter at breast height (Eaton and Lawrence 2006).

Typical stocks of woody debris over succession are unknown due to a paucity of chronosequence studies. Eaton and Lawrence (2006) measured coarse woody debris in forests of different age and land uses in Mexican dry forest. Woody debris stocks in 1–16 year old secondary forests (agricultural fallows) were 5.35–8.61 Mg/ha, with approximately 75% of the total woody debris as coarse in all sites. Using different methods, DeWalt et al. (2003) report downed coarse woody debris increased with forest age, ranging from a volume of 6.5 m^3/ha in 20 year old forest to 35 m^3/ha in old-growth forest. One complication in some of these studies is woody debris is affected by that disturbance histories (e.g., Harmon et al. 1995) as well as by life zone (Delaney et al. 1998), and these often co-vary with secondary forest age.

More data are available on stocks of woody debris in old-growth forests, although studies vary in methodology and whether they report only fallen debris or include standing dead trees. For mature Neotropical forests, values range from 2.43 Mg/ha in a Venezuelan dry forest to 61.44 Mg/ha in floodplain forest (for some examples, see Harmon et al. 1995, Delaney et al. 1998, Clark et al. 2002, 2003, Keller et al. 2004, Rice et al. 2004). In addition, the allocation patterns of woody debris are not well studied. Estimates range from 13.5% to 33% of total aboveground biomass in tropical forests (Harmon et al. 1995, Clark et al. 2002, Eaton and Lawrence 2006). A significant portion of total woody debris biomass may also be in the fine woody fraction ($\leq$ 10 cm diameter); this was estimated to be 25% in Mexican dry forests (Eaton and Lawrence 2006). These numbers indicate that woody debris can be a significant C pool that is often overlooked.

2.7 Trends in Belowground Carbon

2.7.1 Roots

Root biomass during secondary succession has not received as much attention as aboveground biomass. Like other areas, most studies of root biomass compare a single aged forest to a mature forest, or a secondary forest to a plantation (generally monocultures). Thus, there are almost no studies that examine root biomass along a chronosequence (but see Jaramillo et al. 2003 for a 30 years chronosequence), and how patterns of root biomass in mixed species plantation stands compare to those in naturally regenerating stands is generally unknown.

It is hypothesized that early in succession more biomass should be allocated to fine roots and leaves for resource capture, and thus, that ratios of roots to shoots should be greater in younger secondary forests (Yan et al. 2006). Jaramillo et al. (2003) showed that in 8–30 year old secondary forests there was very little biomass allocated to roots below 40 cm in depth, suggesting that these forests may be quite susceptible to disturbances. Hertel et al. (2003) found that secondary montane forests in Costa Rica had shallower organic layers, lower root biomass, and substantially lower nutrients than mature forests. It appears that some forests such as this montane one do not return to biomass levels after several decades of succession, while other forests may (Carvalheiro and Nepstad 1996); however, as mentioned previously our understanding of the recovery process is quite limited. For some recent studies in secondary forests, see Hertel et al. 2003, Jaramillo et al. 2003, Powers 2004, and Adachi et al. 2006. Unfortunately, biomass estimates are difficult to compare among studies due to differences in the definition of fine roots, different sampling depths, and different procedures regarding the separation of live and dead roots.

2.7.2 Soil Carbon

Changes in soil carbon stocks during succession are more difficult to observe than changes in aboveground biomass, because the longer residence time of carbon in the soil may outlast the duration of land use, and because of potential storage at greater depths (beyond 1m) than those usually sampled (Nepstad et al. 1994, Trumbore et al. 1995, Silver et al. 1996). Both net gains and no net change in soil C have been reported with reforestation in the Neotropics (e.g. Mexico, Hughes et al. 1999 and Ecuador, Rhoades et al. 2000). The wide variation in results may be attributed to differences in land use type and intensity, soil properties, and time since land-cover conversion, although the mechanisms for these observed patterns have not been well defined. Land use change can also affect the turnover time and distribution of different soil C fractions, even when changes in the bulk soil C pool are undetectable (Bashkin and Binkley 1998, Binkley and Resh 1999, Marín-Spiotta 2006, see following section on advances in soil methods). In addition to serving as a reservoir for C, soil organic matter (SOM) is a main source of plant nutrients and an important contributor to soil fertility (Tiessen et al. 1994), thus understanding how agricultural abandonment and reforestation affect soil C stocks is important not only for C sequestation but also for restoration of degraded soils.

The type and intensity of prior land use may affect the direction and rate of soil C content change during reforestation (Lugo et al. 1986). In a review of pantropical secondary forests, Silver et al. (2000a) previously reported slower soil C accumulation rates on former croplands than on pastures, opposite to trends observed for aboveground biomass C. Soil C accumulation in cultivated soils may be slower because conventional agricultural practices typically leads to a severe decline in soil C stocks (Mann 1986) relative to pastures, where belowground C inputs may equal or rival those of forests (Fisher et al. 1994, Trumbore et al. 1995, Neill et al. 1997, Schwendenmann and Pendall 2006). Some studies in Costa Rica (Guggenberger and Zech 1999) and Puerto Rico (Lugo et al. 1986, Weaver et al. 1987, Silver et al. 2004) have reported increases in soil C associated with an increase in plant biomass after pasture abandonment. Rhoades et al. (2000) reported that lower montane secondary forests in Ecuador on abandoned sugar cane and pasturelands accumulated soil C at a rate of 1.9 Mg/ha/yr, leading to the recuperation of primary forest soil C stocks in as little as 20 years. In contrast, a study in tropical wet Australia, found long-lasting effects of soil physicochemical changes after pasture use that inhibited recuperation of undisturbed forest soil C stocks (Rasiah et al. 2004). Even after 40 years under abandoned pasture with no grazing, and 30 years of abandoned pasture plus 10 years under replanted forest with native species, soil C stocks remained significantly below those of undisturbed rainforest, likely due to aluminum toxicity and low soil pH.

While aboveground biomass typically increases with secondary forest age (Hughes et al. 1999, Read and Lawrence 2003a), soil C pools often show no relationship with time since agricultural or pasture abandonment, as our data analysis showed. In a seasonally dry region of Mexico, soil C stocks in the top 10 cm did not differ between primary forests, early-successional (10–15 years), mid-successional (20–30 years), or late-successional (60 years) forests regrowing on land formerly cultivated for maize by slash-and-burn (Saynes et al. 2005). Microbial biomass C was greater in early- and mid-successional forests, and also showed seasonal trends. Other studies reported no significant differences in soil C pools between pasture, especially, and secondary or primary forests. In the Cayey mountains of Puerto Rico, gains of new secondary forest C were compensated by losses of pasture-derived C from the soil, resulting in no net change with reforestation or during 80 years of secondary succession (Marín-Spiotta 2006). Using density fractionation and radiocarbon modeling, Marín-Spiotta (2006) found that the majority of soil C was associated with mineral surfaces, which are known to have a stabilizing effect on soil C, and had long residence times, thus the bulk of the C pool was resilient to land-use change. No significant change in soil C stocks has also been reported during secondary succession after abandoned pastures in the Brazilian Amazon (Feldpausch et al. 2004), and slash-and-burn agriculture in Los Tuxtlas, Mexico (Hughes et al. 1999). Hughes et al. (1999) attributed their results to the high C storage capacity of the young volcanic soils in their study sites. These studies suggest that some tropical soils may be resilient to changes in land use and to disturbances that dramatically affect aboveground biomass.

Soil type, in particular differences in texture and mineral content, not only have an effect on bulk soil C content (Post et al. 1982, Eswaran et al. 1993, Neufeldt et al. 2002), but also on its stability and response to land-use change. Using stable C isotopes, López-Ulloa et al. (2005) found that secondary forests on Andisols in northwestern Ecuador lost pasture-derived C and gained forest-derived-C at much faster rates than similarly aged forests on Inceptisols, which appeared to be more insensitive to land-use change.

Land-use history has important effects on soil C stocks, with type and intensity potentially over-riding time since abandonment. A well-replicated study in Ecuador found that the direction of changes in soil C stocks following pasture to forest conversion was best explained by the time a site had been under pasture use (de Koning et al. 2003). Younger pasture soils (< 10 years) had on average 9.3 Mg/ha more soil C than paired secondary forest and plantation sites, while pastures > 20 years had lower soil C content than the forested sites. The difference between pasture and reforested soil C content decreased with pasture age before conversion, pastures 20–30 years old had 18.8 Mg/ha less than forests, and pastures > 30 years had 15.8 Mg/ha less than forests.

The rate and direction of soil C change may vary at different stages of succession, and with soil depth. In a cloud forest chronosequence growing on abandoned maize fields in Oaxaca, Mexico, soils down to 40 cm had the greatest C accumulation rates in the first 15 years of succession, which also coincided with the largest changes in aboveground forest structure. In the next 30 years, the top 20 cm had a net loss of soil C, followed by a smaller increase after 45 years of secondary forest cover (Bautista-Cruz and del Castillo 2005). The lower depths (20–40 cm) showed no patterns with forest age after the first 15 years.

Species composition and diversity can have effects on soil C, in addition to the effects on aboveground biomass discussed previously. Reforestation of native cerrado with pine plantations in Brazil resulted in lower soil C stocks, while reforestation with Eucalyptus increased soil C (Neufeldt et al. 2002). In Hawaii, no net soil C sequestration was documented in young (1 year, Binkley and Resh 1999) or first-rotation (8-year, Binkley et al. 2004) Eucalyptus plantations growing on former sugarcane fields, even after fertilization. Using the natural abundance ^{13}C method, the authors measured equal rates of new plantation C3 inputs and former agricultural C4 soil C losses. Mixed species plantations (Eucalyptus and Albizia, an N-fixer) did, in contrast, accumulate soil C over 17 years, with soil C content positively related to increasing percentage of Albizia stems (Kaye et al. 2000). The authors attributed this to inhibited decomposition of residual sugarcane C in the presence of an N-fixer. Paul et al. (2002) also identified species effects on soil C stocks in plantations established on former cultivated or pastoral lands. Their review suggested that soil C accumulated under hardwoods and some softwoods and nitrogen fixing species, while soil C was lost under some pine plantations.

2.8 Advances in Methods to Study Effects of Land-Use Change on Soil Carbon

Detecting changes in bulk soil C pools with land-use change can be difficult because of the large size of the pool. Differences in methodologies used across studies, including a failure to correct for changes in bulk density associated with changes in soil C concentrations (Veldkamp 1994), also contribute to the wide range of reported results. Estimating changes in C pools by measuring changes in inputs and outputs allows for a more precise assessment of soil C dynamics. Modeling and experimental studies on SOM decomposition and the effects of cultivation on soil C have provided evidence that bulk soil C is a heterogeneous mixture of pools with different chemical properties and residence times in the soil (Jenkinson and Rayner 1977, Parton et al. 1987, Trumbore 1993). As shown in these studies, at least three distinct pools have been identified in soils across biomes and climatic zones: an active or labile pool turning over in one to 5 years, a slow or intermediate pool turning over on a decadal time scale, and a passive pool with turnover time of centuries to millennia. A number of physical and chemical separation methods have been developed to explain the dynamics of the different soil C pools, or soil C fractions (e.g., Greenland and Ford 1964, Elliott and Cambardella 1991, Golchin et al. 1994, Trumbore and

Zheng 1996, Christensen 2001, Paul et al. 2006). Chemical fractionation typically separates soil C pools based on their solubility in water, strong acids, or bases, while physical fractionation methods use differences in density, particle- or aggregate-size.

When coupled with isotopic and other analytical and spectroscopic techniques, fractionation approaches have been successful at describing short- and long-term dynamics of soil C in response to land-use change and other disturbances. Enriched isotope tracers (^{13}C, ^{14}C, ^{15}N) have been applied extensively to track the movement of C or N atoms through different ecosystem components, especially leaf litterfall, microbial biomass, and soil C pools (e.g., Swanston et al. 2002, 2005, Bird et al. 2003, Hanson et al. 2005). Differences in the natural abundance of ^{13}C in C3 and C4 photosynthetic plants can be used to track soil C dynamics when a change in vegetation occurs (Balesdent et al. 1987, Farquhar et al. 1989, Bernoux et al. 1998). For example, in the tropics, most forage grasses in pastures are C4 plants, as are sugarcane and maize crops, while woody plants and forest species are C3. The inputs of different land cover types to SOM can be calculated from differences in ^{13}C /^{12}C ratios (see Vitorello et al. 1989), which can be used as a natural tracer for describing changes in soil C turnover with land-use change in the tropics (Martin et al. 1990, Veldkamp 1994, Neill et al. 1997). In Puerto Rico, Marín-Spiotta (2006) used this technique to show that even though bulk soil C stocks appeared unchanged during a reforestation chronosequence, the SOM pool was not static.

The mean residence time of both above and belowground C stocks can also be estimated from measurements of radiocarbon concentrations in SOM and modeling the decay of ^{14}C emitted from nuclear weapons testing in the 1960s and incorporated into plant biomass during photosynthesis as ^{14}C$-$CO$_2$ (Trumbore 1993, 2000, Chambers et al. 1998). Using stable and radiocarbon isotope analyses of low and high density soil C fractions, de Camargo et al. (1999) found that soil C dynamics in a secondary forest resembled those of a primary forest after 16 years, even though aboveground C had still not recovered primary forest levels. In the same Puerto Rican chronosequence mentioned earlier, Marín-Spiotta (2006) used ^{14}C to estimate faster turnover rates of soil aggregates in pastures than in forests.

Spectroscopic techniques have greatly informed our understanding of the chemical makeup of SOM and of the processes leading to its formation and stabilization in soils. Advances in solid-state cross-polarization ^{13}C- nuclear magnetic resonance spectroscopy (NMR) spectroscopy allow for the study of SOM in situ without chemical modification (Kögel-Knabner 2000, Preston 2001, Helfrich et al. 2006). ^{13}C-NMR can provide a first approximation of the relative abundance of organic C functional groups, such as alkyl, O-alkyl, aromatic and carbonyl C, which can be used as indicators for the presence of different compounds, such as carbohydrates, proteins, lignin, lipids, and charred materials (see Baldock et al. 2004). This method, combined with physical fractionation, has been applied successfully to identify chemical changes in different soil C fractions with land-use change across a wide range of climates and soil types (Oades et al. 1988, Golchin et al. 1994, 1995, Guggenberger et al. 1995a, 1995b, Helfrich et al. 2006). Other methods for SOM characterization are Fourier transform infrared spectroscopy (FTIR) and pyrolysis gas chromatography/mass spectrometry (GC/MS). Nierop et al. (2001)

used pyGC/MS to determine the source and degree of decomposition of soil C profiles under organic farming, conventional tilling and pasture. Coupled with isotope ratio MS, pyrolysis-GC/MS has shed light on the fate of individual compound groups during the incorporation of plant litter into SOM (Gleixner et al. 1999).

Chromatographic techniques, such as XAD fractionation (Croué 2004), solid-phase extraction on C-18 columns (Louchouarn et al. 2000), and high-pressure size exclusion chromatography (Chin et al. 1994) are useful for separating soil extracts and dissolved organic matter from plants and in soils by polarity and molecular weight, properties which are related to chemical recalcitrance and decomposability. Generally, low-molecular weight and hydrophobic compounds are thought to represent the most labile fractions of plant litter and SOM (carbohydrates, amino acids, small proteins, organic acids), while the high-molecular weight and hydrophobic compounds represent more recalcitrant materials. These types of compounds identified by chromatography columns have been shown to accumulate under different vegetation types and land-use regimes (Sanger et al. 1997). These and other analytical techniques which can be used to enhance our understanding of soil C dynamics with land-use change have been reviewed recently by Kögel-Knabner (2000), Northcott and Jones (2000) and Poirier et al. (2005).

Results from the studies mentioned above and others using these techniques suggest that bulk soil C measurements are often too coarse to detect changes over forest successional time periods, and may lead to the erroneous conclusion that the soil C pool has not responded to land-use change. The soil C fraction most sensitive to land-use is typically the low density, particulate C fraction, also known as the labile or active pool (Cambardella and Elliott 1993, Alvarez et al. 1998, Guggenberger and Zech 1999, Compton and Boone 2000, Baisden et al. 2002, John et al. 2005, Helfrich et al. 2006). While perhaps making up a small proportion of the total C pool, the light fraction may cycle large amounts of C and thus dominate soil-atmosphere feedback interactions (McGroddy and Silver 2000). A number of studies have detected changes in the distribution and chemistry of different soil C fractions, even when the bulk soil C pool appeared unchanged in tropical, temperate and boreal soils (Binkley and Resh 1999, Neff et al. 2002, Li et al. 2005, Marín-Spiotta 2006). The implementation of physical and chemical fractionation, isotopic and spectroscopic techniques, has increased our understanding of the composition and location of C compounds in the soil organo-mineral matrix, and elucidated many of the chemical, physical and biological stabilization mechanisms controlling root biomass and soil C formation and turnover. The application of these methods to soil C studies in the tropics, however, is still limited.

2.9 Future of Secondary Forests

The C sequestration potential of secondary forests depends on their future fate. As the area of secondary forest cover increases, these will become the main source of land available for future human use. In many regions, most secondary forests are in a fallow stage, that is, they have only temporarily been taking out of the production cycle, so reconversion to non-forest land uses is highly likely (Kammesheidt 2002, Schroth et al. 2002, Walker 2003, Soares-Filho et al. 2004). In Asia, the length of time of swidden fallow secondary forest systems is decreasing, and these are increasingly being converted to cash-crop and cash-tree plantations (de Jong et al. 2001). The age of secondary forests in the Colombian lowland landscape is also increasingly becoming younger (Etter et al. 2005), implying that secondary forests are experiencing multiple cycles of disturbance. With increasing frequency of disturbance, the potential for net loss of C as CO_2 to the atmosphere increases. In regions where the economy has shifted from agriculture to an industrial or service-based economy, such as in Puerto Rico, conversion to agriculture or pasture is no longer a likely threat to secondary forests. Instead, these are being increasingly cleared for urban uses, such as residential and commercial development, or golf courses (Thomlinson and Rivera 2000, Helmer 2004).

Secondary forests have been traditionally undervalued, particularly due to the predominance of exotic species, and so they typically fall below the radar of conservationists and environmental planners. Although species composition of secondary forests may not return to that of primary forests (Lugo and Helmer 2004), there is increasingly more evidence that secondary forests can reach structural and potentially functional characteristics of primary forests in as little as 20 years (Brown and Lugo 1990, Guariguata and Ostertag 2001). The important role of secondary forests in C sequestration, in restoration of forest ecosystem goods and services, and as habitat for biodiversity in fragmented landscapes (Dunn 2004, Veddeler et al. 2005) is increasingly being recognized.

2.10 Summary and Recommendations for Future Studies

We compiled data on aboveground biomass and soil C stocks from Neotropical secondary forests and plantations growing on former agricultural or pasturelands and examined the effect of time since abandonment on C accumulation. Our analysis showed that the predictive power of time since abandonment on soil C stocks was very low. We review a number of studies that did not find changes in soil C with site age. Land-use history (type and intensity), frequency of disturbance, and the use of fire, are potentially more important than regenerative time for determining success, direction, and rates of C sequestration belowground. An identification of these factors at the landscape level coupled with the creation or enforcement of regional land use and zoning plans is important for predicting where resources for reforestation should be focused. In many areas, forest regrowth will occur unassisted in a relatively short timescale. When barriers exist to natural regeneration, conversion to plantations or managed restoration can facilitate the recovery of aboveground biomass. The conservation value of secondary forests needs to be better explored at the landscape level as well, and incorporated into environmental and agricultural planning.

Studies that combine isotopic and molecular techniques with more traditional ecological methods increase our ability to detect changes in soil C stocks and better understand soil C dynamics with land-use change. The application of these techniques to studies in the tropics is still limited. Our understanding of the factors controlling root biomass and soil C with reforestation is a lot less than those on aboveground dynamics. There are many studies across the tropics on different aspects of regeneration, species diversity, seedling survival, structural characteristics (stem density, basal area), but a lot fewer examine soil C. We encourage interdisciplinary collaborations between plant and community ecologists and biologists with soil scientists and chemists to provide a more comprehensive picture of forest dynamics with reforestation. Soil studies should report carbon content on a per area basis or carbon concentrations with bulk density values for the proper conversion to carbon content. Unfortunately, too many studies report %C (or %N) alone per depth, when potential changes in bulk density, especially during land-use change, hinder comparisons of concentrations across treatments.

Unlike for soil C, it is clear that the potential for C accumulation aboveground is high during secondary succession in Neotropical forests, and C accumulation follows a log-linear pattern, with rapid early accumulation. This C accumulation reaches an eventual plateau, which appears to occur within 50 years in dry forests, but can take over 100 years on wet and moist forests. Given similar land use histories, wet tropical forests clearly have the greatest potential for aboveground C accumulation. Our data also suggest that lands that are cleared and rapidly returned to successional processes have the potential to accumulate more C over time than lands that have been in sustained agriculture or pasture. A previous study found that agricultural lands had slightly greater potential for forest regeneration (Silver et al. 2000a), and the authors suggested that these lands were selected for agriculture because they were the richest in soil nutrients. This effect appears to be dependent on the length of time land is held in agriculture, so it may be useful to focus reforestation efforts on areas with minimal time since conversion.

Most studies on aboveground dynamics with reforestation also report basal area, and few report biomass stocks. We encourage authors to attempt to provide biomass values using published allometric equations. While using allometric equations certainly has its caveats and sources of uncertainty, these have been well identified and there is a very large number of biomass equations available for different forest types and life zones, especially for Neotropical sites. The dry tropics are a particularly understudied life zone. We also found almost twice as many studies conducted in the first 20 years after abandonment, but our data shows that older forests may behave differently, so it is important to include sites beyond the first two decades whenever available. As the age of secondary forests decreases, these older secondary forests are becoming a threatened habitat, like primary forests.

Appendices

Appendix 2.1 Aboveground C pools in secondary forests and plantations of known age following abandonment of agricultural and pasturelands and in nearby mature forests in the Neotropics. Life zones are wet (W), moist (M), and dry (D) based on mean annual precipitation descriptions given by authors. Past land uses are agriculture (A), pasture (P). Cover types are secondary forests (S) or plantations (P). Plantations are identified as mixed (M) or single species (S), and native (N) or exotic (E). Aboveground C was calculated as 50% of dry biomass

Age (y)	Life zone	Past Land use	Cover Type	Mixed vs. Single spp	Native vs. exotic	Aboveground Biomass C (Mg/ha)	Location	Reference
0.3	M	A	S			2	Peru	Szott et al. 1994
0.5	W	A	S			1	Mexico	Hughes et al. 1999
0.7	M	A	S			2	Peru	Szott et al. 1994
0.8	M	A	S			2	Guatemala	Tergas and Popenoe 1971
0.8	M	A	S			5	Guatemala	Tergas and Popenoe 1971
0.8	M	A	S			6	Guatemala	Tergas and Popenoe 1971
0.8	M	A	S			50	Guatemala	Tergas and Popenoe 1971
0.8	M	A	S			5	Guatemala	Tergas and Popenoe 1971
0.8	M	A	S			4	Guatemala	Tergas and Popenoe 1971
0.8	M	A	S			2	Guatemala	Tergas and Popenoe 1971
0.8	M	A	S			7	Guatemala	Tergas and Popenoe 1971
0.8	M	A	S			7	Guatemala	Tergas and Popenoe 1971
0.8	M	A	S			7	Guatemala	Tergas and Popenoe 1971
0.8	W	A	S			2	Mexico	Williams-Linera 1983
1	M	A	S			4	Guatemala	Snedaker 1970
1	M	A	S			3	Brazil	Uhl et al. 1988
1	W	C	S			3	Puerto Rico	Silver et al. 1996
1	W	A	S			4	Brazil	Uhl 1987
1.3	M	A	S			4	Brazil	Gehring et al. 1999
1.4	M	A	S			7	Peru	Szott et al. 1994
1.9	M	A	S			6	Brazil	Gehring et al. 1999

2	D	A	S	6	Mexico	Read and Lawrence 2003
2	M	A	S	4	Brazil	Alves et al. 1997
2	M	A	S	6	Costa Rica	Ewel 1971
2	M	S		9	Colombia	Folster et al 1976
2	M	C	S	30	Brazil	Gehring et al. 2005
2	M	A	S	36	Brazil	Lucas et al. 2002
2	M	A	S	7	Guatemala	Snedaker 1970
2	W	A	S	6	Brazil	Uhl 1987
2.3	M	A	S	6	Brazil	Gehring et al. 1999
2.4	M	A	S	12	Peru	Szott et al. 1994
2.5	M	P	S	8	Brazil	Uhl et al. 1988
2.5	M	P	S	4	Brazil	Uhl et al. 1988
2.8	M	C	S	17	French Guyana	Maury-Lechon 1982
3	D	A	S	3	Mexico	Read and Lawrence 2003
3	D	A	S	5	Mexico	Read and Lawrence 2003
3	M	A	S	19	Brazil	Alves et al. 1997
3	M	A	S	17	Brazil	Alves et al. 1997
3	M	C	S	50	Brazil	Gehring et al. 2005
3	M	A	S	11	Guatemala	Snedaker 1970
3	W	A	S	10	Brazil	Uhl 1987
3	W	C	S	4	Brazil	Uhl et al. 1982
3	W	C	S	0	Brazil	Uhl et al. 1982
3	W	C	S	6	Brazil	Uhl et al. 1982
3.5	M	P	S	8	Brazil	Uhl et al. 1988
3.5	M	P	S	15	Brazil	Uhl et al. 1988
3.5	M	P	S	4	Brazil	Uhl et al. 1988
3.6	M	A	S	20	Peru	Szott et al. 1994
4	D	A	S	4	Mexico	Read and Lawrence 2003
4	D	A	S	3	Mexico	Read and Lawrence 2003
4	M	A	S	19	Costa Rica	Ewel 1971
4	M	A	S	21	Mexico	Hughes et al. 1999
4	M	P/A	S	24	Brazil	Lucas et al. 2002

(continued)

Appendix 2.1 (continued)

Age (y)	Life zone	Past Land use	Cover Type	Mixed vs. Single spp	Native vs. exotic	Aboveground Biomass C (Mg/ha)	Location	Reference
4	M	A	S			14	Guatemala	Snedaker 1970
4	M	P	S			9	Brazil	Uhl et al. 1988
4	W		P	S	E	20	Puerto Rico	Lugo 1992
4	W	A	S			14	Brazil	Uhl 1987
4.4	M	A	S			27	Peru	Szott et al. 1994
4.5	M	P	S			27	Brazil	Uhl et al. 1988
5	D	A	S			4	Mexico	Read and Lawrence 2003
5	D	A	S			9	Mexico	Read and Lawrence 2003
5	D	A	S			16	Mexico	Read and Lawrence 2003
5	D	A	S			8	Mexico	Read and Lawrence 2003
5	D	A	S			6	Mexico	Read and Lawrence 2003
5	M	A	S			19	Brazil	Alves et al. 1997
5	M		S			34	Colombia	Folster et al 1976
5	M	C	S			65	Brazil	Gehring et al. 2005
5	M	A	S			18	Guatemala	Snedaker 1970
5	W	A	S			17	Brazil	Uhl 1987
5.5	W		S			16	Puerto Rico	Lugo 1992
6	D	A	S			5	Mexico	Read and Lawrence 2003
6	M	P	S			3	Brazil	Davidson et al. 2004
6	M	A	S			21	Costa Rica	Ewel 1971
5	W	A	S			17	Brazil	Uhl 1987
5.5	W		S			16	Puerto Rico	Lugo 1992
6	D	A	S			5	Mexico	Read and Lawrence 2003
6	M	P	S			3	Brazil	Davidson et al. 2004
6	M	A	S			21	Costa Rica	Ewel 1971
6	M	A	S			22	Guatemala	Snedaker 1970
7	D	A	S			3	Mexico	Read and Lawrence 2003
7	M	P	S			4	Brazil	Davidson et al. 2004

7	M	C	S		75	Brazil	Gehring et al. 2005
7	M	C	S		35	Brazil	Lucas et al. 2002
7	M	A	S		23	Guatemala	Snedaker 1970
7	W	P	S		3	Puerto Rico	Aide et al. 1995
7	W	A	S		22	Mexico	Williams-Linera 1983
7.5	M	P	S		19	Brazil	Uhl et al. 1988
8	D	A	S		7	Mexico	Read and Lawrence 2003
8	D	A	S		5	Mexico	Read and Lawrence 2003
8	D	A	S		6	Mexico	Read and Lawrence 2003
8	D	A	S		16	Mexico	Read and Lawrence 2003
8	M	P	S		4.8	Brazil	Davidson et al. 2004
8	M	P/A	S		52	Brazil	Lucas et al. 2002
8	M	A	S		33	Guatemala	Snedaker 1970
8	M	P	S		44	Brazil	Uhl et al. 1988
8	M	P	S		43	Brazil	Uhl et al. 1988
8	M	P	S		16	Brazil	Uhl et al. 1988
8	M	P	S		2	Brazil	Uhl et al. 1988
8	W	A	S		11	Mexico	Hughes et al. 1999
8	W	P	S		49	Mexico	Hughes et al. 1999
9	D	A	S		5	Mexico	Read and Lawrence 2003
9	M	A	S		45	Brazil	Alves et al. 1997
9	M	C	S		67	Brazil	Lucas et al. 2002
9	M	C	S		65	Brazil	Lucas et al. 2002
9	M	C	S		57	Brazil	Lucas et al. 2002
9	M	C	S		59	Brazil	Lucas et al. 2002
9	M	C	S		57	Brazil	Lucas et al. 2002
9	M	C	S		62	Brazil	Lucas et al. 2002
9	M	C	S		56	Brazil	Lucas et al. 2002
9	M	C	S		62	Brazil	Lucas et al. 2002
9	M	A	S		22	Colombia/Venezuela	Saldarriaga et al. 1988
9	M	A	S		36	Guatemala	Snedaker 1970

(continued)

Appendix 2.1 (continued)

Age (y)	Life zone	Past Land use	Cover Type	Mixed vs. Single spp	Native vs. exotic	Aboveground Biomass C (Mg/ha)	Location	Reference
10	D	A	S			10	Mexico	Read and Lawrence 2003
10	M	C	S			80	Brazil	Gehring et al. 2005
10	M	A	S			27	Guatemala	Snedaker 1970
10	W	P	S			7	Puerto Rico	Marin-Spiotta et al. in press
10	W	P	S			2	Puerto Rico	Marin-Spiotta et al. in press
10	W	P	S			1	Puerto Rico	Marin-Spiotta et al. in press
11	M	P	S			32	Brazil	Alves et al. 1997
11	M	A	S			26	Colombia/Venezuela	Saldarriaga et al. 1988
11	W	A	S			18	Puerto Rico	Cuevas et al. 1991
12	D	A	S			11	Brazil	Read and Lawrence 2003
12	D	A	S			14	Brazil	Read and Lawrence 2003
12	D	A	S			15	Brazil	Read and Lawrence 2003
12	M	C	S			55	Brazil	Lucas et al. 2002
12	M	A	S			41	Colombia/Venezuela	Saldarriaga et al. 1988
12	W	P	S			3	Puerto Rico	Aide et al. 1995
13	W	P	P	M	N	32	Costa Rica	Redondo-Brenes and Montagnini, 2006
13	W	P	P	S	N	25	Costa Rica	Redondo-Brenes and Montagnini, 2007
14	M	A	S			27	Colombia/Venezuela	Saldarriaga et al. 1988
14	W	A	S			40	Brazil	Schroth et al. 2002
15	D	A	S			9	Mexico	Read and Lawrence 2003
15	M	P	S			23	Ecuador	Fehse et al 2002
16	D	A	S			13	Brazil	Read and Lawrence 2003
16	M		S			52	Brazil	Alves et al. 1997
16	M		S			101	Colombia	Folster et al 1976
16	M	C	S			58	Brazil	Lucas et al. 2002
16	W	A	S			136	Mexico	Hughes et al. 1999

17	M	P	S			22	Brazil	de Koning et al. 1999
17	W	A	P	S	E	50	Hawai'I	Kaye et al. 2000
17	W	A	P	M	E	85	Hawai'I	Kaye et al. 2000
17	W		P	S	E	51	Puerto Rico	Lugo 1992
18	D	A	S			13	Mexico	Read and Lawrence 2003
18	D	A	S			7	Mexico	Read and Lawrence 2003
18	M		S			72	Brazil	Alves et al. 1997
18.5	W		P	S	E	85	Puerto Rico	Lugo 1992
20	M	C	S			100	Brazil	Gehring et al. 2005
20	M	A	S			31	Colombia/Venezuela	Saldarriaga et al. 1988
20	M	A	S			49	Colombia/Venezuela	Saldarriaga et al. 1988
20	M	A	S			32	Colombia/Venezuela	Saldarriaga et al. 1988
20	M	A	S			42	Colombia/Venezuela	Saldarriaga et al. 1988
20	W		P	S	E	60	Panama	Kraenzel et al. 2003
20	W	A	S			38	Mexico	Hughes et al. 1999
20	W	A	S			127	Mexico	Hughes et al. 1999
20	W	P	S			75	Puerto Rico	Marin-Spiotta et al. in press
20	W	P	S			84	Puerto Rico	Marin-Spiotta et al. in press
20	W	P	S			43	Puerto Rico	Marin-Spiotta et al. in press
21	M	C	S			109	Brazil- AMZ	Lucas et al. 2002
22	W	P	S			15	Puerto Rico	Aide et al. 1995
22.5	W		S			36	Puerto Rico	Lugo 1992
22.5	W		S			55	Puerto Rico	Lugo 1992
24	D	A	S			24	Mexico	Read and Lawrence 2003
25	D	A	S			23	Mexico	Read and Lawrence 2003
25	D	A	S			15	Mexico	Read and Lawrence 2003
25	M	C	S			115	Brazil	Gehring et al. 2005
25	W	P	S			44	Puerto Rico	Aide et al. 1995
26	W	A	S			100	Mexico	Hughes et al. 1999
30	M	C	S			146	Brazil	Lucas et al. 2002
30	M	A	S			27	Colombia/Venezuela	Saldarriaga et al. 1988
30	W	A	S			121	Mexico	Hughes et al. 1999

(continued)

Appendix 2.1 (continued)

Age (y)	Life zone	Past Land use	Cover Type	Mixed vs. Single spp	Native vs. exotic	Aboveground Biomass C (Mg/ha)	Location	Reference
30	W	P	S			39	Puerto Rico	Marin-Spiotta et al. in press
30	W	P	S			48	Puerto Rico	Marin-Spiotta et al. in press
30	W	P	S			45	Puerto Rico	Marin-Spiotta et al. in press
35	M	A	S			55	Colombia/Venezuela	Saldarriaga et al. 1988
35	M	A	S			54	Colombia/Venezuela	Saldarriaga et al. 1988
40	M	A	S			80	Colombia/Venezuela	Saldarriaga et al. 1988
44	M		S			83	Puerto Rico	Jordan and Farnsworth 1982
49	W		P	S	E	62	Puerto Rico	Lugo 1992
50	W	A	S			137	Mexico	Hughes et al. 1999
50	W		S			40	Puerto Rico	Lugo 1992
54	M	P	S			79	Puerto Rico	Silver et al. 2004
60	M	A	S			58	Colombia/Venezuela	Saldarriaga et al. 1988
60	M	A	S			99	Colombia/Venezuela	Saldarriaga et al. 1988
60	M	A	S			69	Colombia/Venezuela	Saldarriaga et al. 1988
60	W	P	P		both	40	Puerto Rico	Silver et al. 2004
60	W	P	S			33	Puerto Rico	Aide et al. 1995
60	W	P	S			54	Puerto Rico	Aide et al. 1995
60	W	P	S			87	Puerto Rico	Marin-Spiotta et al. in press
60	W	P	S			77	Puerto Rico	Marin-Spiotta et al. in press
60	W	P	S			83	Puerto Rico	Marin-Spiotta et al. in press

80	M	A	S		67	Colombia/Venezuela	Saldarriaga et al. 1988
80	M	A	S		89	Colombia/Venezuela	Saldarriaga et al. 1988
80	M	A	S		72	Colombia/Venezuela	Saldarriaga et al. 1988
80	M	A	S		71	Colombia/Venezuela	Saldarriaga et al. 1988
80	W	P	S		93	Puerto Rico	Marin-Spiotta et al. in press
80	W	P	S		152	Puerto Rico	Marin-Spiotta et al. in press
80	W	P	S		156	Puerto Rico	Marin-Spiotta et al. in press
Mature	D	A	S		30	Mexico	Read and Lawrence 2003
Mature	D	A	S		35	Mexico	Read and Lawrence 2003
Mature	D	A	S		31	Mexico	Read and Lawrence 2003
Mature	D	A	S		41	Mexico	Read and Lawrence 2003
Mature	D	A	S		33	Mexico	Read and Lawrence 2003
Mature	D	A	S		39	Mexico	Read and Lawrence 2003
Mature	D	A	S		34	Mexico	Read and Lawrence 2003
Mature	D	A	S		30	Mexico	Read and Lawrence 2003
Mature	M	P	S		132	Brazil	de Koning et al. 1999
Mature	M	C	S		229	Brazil	Gehring et al. 2005
Mature	W	P	S		84	Puerto Rico	Marin-Spiotta et al. in press
Mature	W	P	S		92	Puerto Rico	Marin-Spiotta et al. in press
Mature	W	P	S		66	Puerto Rico	Marin-Spiotta et al. in press

Appendix 2.2 Soil C pools in secondary forests and plantations of known age following abandonment of agricultural and pasturelands and in nearby mature forests in the Neotropics. Depth refers to maximum soil depth reported for the measurement of soil C content. Soil C 0-25 cm are soil C values adjusted to a common depth using a regression approach (see text). Life zones are wet (W), moist (M), and dry (D) based on mean annual precipitation descriptions given by authors. Past land uses are agriculture (A), pasture (P). Cover types are secondary forests (S) or plantations (P)

Age (y)	Depth (cm)	Life Zone	Past Land Use	Cover type	Soil C (Mg/ha)	Soil C 0–25 cm (Mg/ha)	Location	Reference
4	30	W	A	S	116	100	Mexico	Hughes et al. 1999
4	100	W		P	44	14	Puerto Rico	Lugo 1992
5	40	M	A	S	45	47	Brazil	Sommer et al. 2000
5	45	M	P	S	65	64	Brazil	Feldpausch et al. 2004
5	10	W	P	S	14	30	Costa Rica	Reiners et al. 1994
5	30	W	P/A	P	77	66	Panama	Potvin et al. 2004
5.5	100	W		S	39	12	Puerto Rico	Lugo 1992
6	10	M	P	S	51	110	Dominican Republic	Templer et al. 2005
7	25	M	P	S/P	62	62	Ecuador	de Koning et al. 2003
7	45	M	P	S	68	67	Brazil	Feldpausch et al. 2004
7	20	W	C	S	75	90	Mexico	Williams-Linera 1983
7	25	W	P	S/P	52	52	Ecuador	de Koning et al. 2003
7	30	W	P	P	85	73	Costa Rica	Powers 2004
8	25	M	P	S/P	55	55	Ecuador	de Koning et al. 2003
8	25	M	P	S/P	52	52	Ecuador	de Koning et al. 2003
8	50	M	P	S	65	61	Brazil	Buschbacher et al. 1988
8	50	M	P	S	68	64	Brazil	Buschbacher et al. 1988
8	50	M	P	S	70	66	Brazil	Buschbacher et al. 1988
8	25	W	P	S/P	60	60	Ecuador	de Koning et al. 2003
8	30	W	A	S	71	61	Mexico	Hughes et al. 1999
8	30	W	P	S	120	103	Mexico	Hughes et al. 1999
8	45	W	A	P	135	82	Hawaii	Binkley et al. 2004
9	25	M	P	S/P	59	59	Ecuador	de Koning et al. 2003

9	10	W	P	S	13	28	Costa Rica	Reiners et al. 1994
9	10	W	P	S	19	41	Costa Rica	Reiners et al. 1994
9	15	W	A	P	32	49	Costa Rica	Russell et al. 2004
9	15	W	A	P	35	54	Costa Rica	Russell et al. 2004
9	15	W	A	P	34	52	Costa Rica	Russell et al. 2004
9	15	W	A	P	37	57	Costa Rica	Russell et al. 2004
9	15	W	A	P	38	58	Costa Rica	Russell et al. 2004
9	15	W	A	P	41	63	Costa Rica	Russell et al. 2004
10	25	M	P	S/P	69	69	Ecuador	de Koning et al. 2003
10	25	M	P	S/P	55	55	Ecuador	de Koning et al. 2003
10	25	M	P	S/P	76	76	Ecuador	de Koning et al. 2003
10	25	M	P	S/P	80	80	Ecuador	de Koning et al. 2003
10	30	M	P	S	103	126	Puerto Rico	Marin-Spiotta 2006
10	30	M	P	S	67	82	Puerto Rico	Marin-Spiotta 2006
10	30	M	P	S	84	103	Puerto Rico	Marin-Spiotta 2006
10	30	M	A	S	57	70	Honduras	Paniagua et al. 1999
10	20	W	A	S	32	39	Brazil	Johnson et al. 2001
10	25	W	A	P	70	70	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
10	25	W	P	S/P	73	73	Ecuador	de Koning et al. 2003
10	25	W	P	S/P	99	99	Ecuador	de Koning et al. 2003
10	25	W	A	P	60	60	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
11	25	D	C	S	50	50	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
11	10	M	P	S	23	50	Brazil	Salimon et al. 2004
11	25	M	P	S/P	46	46	Ecuador	de Koning et al. 2003
11	25	W	P	S/P	71	71	Ecuador	de Koning et al. 2003
11	25	W	P	S/P	69	69	Ecuador	de Koning et al. 2003
11	30	W	P	P	41	35	Puerto Rico	Cuevas et al. 1991
11	30	W	C	S	42	36	Puerto Rico	Cuevas et al. 1991
12	40	M	A	S	44	46	Brazil	Sommer et al. 2000
12	10	W	P	S	21	45	Costa Rica	Reiners et al. 1994
12	10	W	C	S	22	47	Costa Rica	Reiners et al. 1994

(continued)

Appendix 2.2 (continued)

Age (y)	Depth (cm)	Life Zone	Past Land Use	Cover type	Soil C (Mg/ha)	Soil C 0–25 cm (Mg/ha)	Location	Reference
12	25	W	A	P	72	72	Hawaii	Bashkin and Binkley 1998
12.5	10	D	A	S	39	67	Mexico	Saynes et al. 2005
13	45	M	P	S	74	73	Brazil	Feldpausch et al. 2004
13	25	W	P	S/P	74	74	Ecuador	de Koning et al. 2003
14	25	M	P	S/P	78	78	Ecuador	de Koning et al. 2003
15	20	M	A	S	98	148	Mexico	Bautista-Cruz and del Castillo 2005
15	20	M	A	S	162	245	Mexico	Bautista-Cruz and del Castillo 2005
15	20	M	A	S	136	205	Mexico	Bautista-Cruz and del Castillo 2005
15	25	M	P	S/P	63	63	Ecuador	de Koning et al. 2003
15	25	M	P	S/P	100	100	Ecuador	de Koning et al. 2003
15	25	M	P	S/P	66	66	Ecuador	de Koning et al. 2003
15	25	M	P	S/P	64	64	Ecuador	de Koning et al. 2003
15	25	M	P	S/P	116	116	Ecuador	de Koning et al. 2003
15	5	W	P	S	33	128	Ecuador	Fehse et al. 2002
15	10	W	C	S	21	45	Costa Rica	Reiners et al. 1994
15	25	W	P	S/P	64	64	Ecuador	de Koning et al. 2003
15	25	W	P	S/P	108	108	Ecuador	de Koning et al. 2003
15	25	W	P	S/P	95	95	Ecuador	de Koning et al. 2003
16	25	M	P	S/P	40	40	Ecuador	de Koning et al. 2003
16	25	W	P	S/P	104	104	Ecuador	de Koning et al. 2003
16	30	W	P	S	77	66	Costa Rica	Guariguata et al. 1997
16	30	W	A	S	92	79	Mexico	Hughes et al. 1999
16	30	W	P	S	44	38	Costa Rica	Werner 1984
16.5	30	W	P	S	79	68	Costa Rica	Guariguata et al. 1997
17	10	M	P	S	25	54	Brazil	de Camargo et al. 1999
17	100	M		P	93	61	Puerto Rico	Lugo 1992
17	25	W	P	S/P	93	93	Ecuador	de Koning et al. 2003
17	25	W	P	S/P	75	75	Ecuador	de Koning et al. 2003

17	30	W	P	S	114	98	Costa Rica	Guariguata et al. 1997
17	50	W	A	P	127	71	Hawaii	Kaye et al. 2000
17	50	W	A	P	127	71	Hawaii	Kaye et al. 2000
17	50	W	A	P	135	75	Hawaii	Kaye et al. 2000
17	50	W	A	P	145	81	Hawaii	Kaye et al. 2000
17	50	W	A	P	148	83	Hawaii	Kaye et al. 2000
17	50	W	A	P	128	72	Hawaii	Kaye et al. 2000
17.5	30	W	P/A	S	129	111	Ecuador	Rhoades et al. 2000
17.5	30	W	P/A	S	101	87	Ecuador	Rhoades et al. 2000
18	25	D	P	S/P	59	59	Ecuador	de Koning et al. 2003
18.5	100	W		P	89	28	Puerto Rico	Lugo 1992
19	25	W	P	S	49	49	Puerto Rico	Lugo et al. 1986
20	25	M	P	S/P	79	79	Ecuador	de Koning et al. 2003
20	30	M	P	S	103	126	Puerto Rico	Marin-Spiotta 2006
20	30	M	P/A	S	45	55	Puerto Rico	Marin-Spiotta 2006
20	30	M	P	S	67	82	Puerto Rico	Marin-Spiotta 2006
20	20	W	A	S	25	30	Brazil	Johnson et al. 2001
20	25	W	P	S/P	98	98	Ecuador	de Koning et al. 2003
20	25	W	A	S	57	57	Puerto Rico	Li et al. 2005
20	25	W	A	P	56	56	Puerto Rico	Li et al. 2005
20	30	W	A	S	103	88	Mexico	Hughes et al. 1999
20	30	W	A	S	87	75	Mexico	Hughes et al. 1999
20	70	W		P	110	46	Panama	Kraenzel et al. 2003
21	25	W	P	S/P	83	83	Ecuador	de Koning et al. 2003
22.5	100	M		S	61	40	Puerto Rico	Lugo 1992
22.5	100	W		S	86	27	Puerto Rico	Lugo 1992
23	20	M	C	P	117	177	Brazil	Smith et al. 1998
23	25	W	A	S	65	65	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
23	25	W	P	S	47	47	Puerto Rico	Lugo et al. 1986
25	10	D	A	S	39	67	Mexico	Saynes et al. 2005

(continued)

Appendix 2.2 (continued)

Age (y)	Depth (cm)	Life Zone	Past Land Use	Cover type	Soil C (Mg/ha)	Soil C 0–25 cm (Mg/ha)	Location	Reference
25	10	W	A	S	90	194	Jamaica	McDonald and Healey 2000
25	25	W	P	S/P	57	57	Ecuador	de Koning et al. 2003
25	25	W	P	S/P	54	54	Ecuador	de Koning et al. 2003
25	25	W	P	S/P	58	58	Ecuador	de Koning et al. 2003
25	25	W	P	S/P	65	65	Ecuador	de Koning et al. 2003
26	25	M	A	S	40	40	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
26	30	W	A	S	82	70	Mexico	Hughes et al. 1999
30	25	M	P	S/P	57	57	Ecuador	de Koning et al. 2003
30	25	M	P	S	23	23	Puerto Rico	Lugo et al. 1986
30	30	M	P	S	79	97	Puerto Rico	Marin-Spiotta 2006
30	30	M	P	S	56	68	Puerto Rico	Marin-Spiotta 2006
30	30	M	P	S	42	51	Puerto Rico	Marin-Spiotta 2006
30	25	W	P	S/P	58	58	Ecuador	de Koning et al. 2003
30	30	W	A	S	117	100	Mexico	Hughes et al. 1999
31	30	W	A	S	43	37	Costa Rica	Werner 1984
35	25	D	A	S	75	75	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
35	25	D	P	S	77	77	Puerto Rico	Lugo et al. 1986
36	20	M	C	P	92	139	Brazil	Smith et al. 1998
36	20	M	C	P	93	140	Brazil	Smith et al. 1998
36	20	M	C	P	95	143	Brazil	Smith et al. 1998
40	25	M	P	S	70	70	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
40	40	M	A	S	50	53	Brazil	Sommer et al. 2000
40	20	W	A	S	22	27	Brazil	Johnson et al. 2001
40	25	W	A	S	75	75	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
40	25	W	P	S	60	60	Puerto Rico	Lugo et al. 1986
42.5	25	W	A	S	83	83	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
45	20	M	A	S	130	196	Mexico	Bautista-Cruz and del Castillo 2005
45	20	M	A	S	90	136	Mexico	Bautista-Cruz and del Castillo 2005
45	20	M	A	S	135	204	Mexico	Bautista-Cruz and del Castillo 2005
49	100	W		P	45	14	Puerto Rico	Lugo 1992

50	25	D	A	P	90	90	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
50	25	D	P	S	90	90	Puerto Rico	Lugo et al. 1986
50	100	W		S	81	25	Puerto Rico	Lugo 1992
51	25	W	A	P	80	80	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
55	25	M	A	S	80	80	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
60	10	D	A	S	41	70	Mexico	Saynes et al. 2005
60	30	M	P	S	61	75	Puerto Rico	Marin-Spiotta 2006
60	30	M	P	S	64	78	Puerto Rico	Marin-Spiotta 2006
60	30	M	P	S	60	73	Puerto Rico	Marin-Spiotta 2006
61	10	M	P	S	43	93	Puerto Rico	Silver et al. 2004
61	30	M	P	S	78	95	Puerto Rico	Silver et al. 2004
75	20	M	A	S	135	204	Mexico	Bautista-Cruz and del Castillo 2005
75	20	M	A	S	105	159	Mexico	Bautista-Cruz and del Castillo 2005
75	20	M	A	S	126	190	Mexico	Bautista-Cruz and del Castillo 2005
80	30	M	P	S	97	119	Puerto Rico	Marin-Spiotta 2006
80	30	M	P	S	49	60	Puerto Rico	Marin-Spiotta 2006
80	30	M	P	S	59	72	Puerto Rico	Marin-Spiotta 2006
100	25	M	A	S	80	80	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
Mature	10	D			36	62	Mexico	Saynes et al. 2005
Mature	25	D			60	60	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
Mature	25	D			45	45	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
Mature	10	M			26	56	Brazil	de Camargo et al. 1999
Mature	10	M			18	39	Brazil	Salimon et al. 2004
Mature	10	M			23	50	Brazil	Salimon et al. 2004
Mature	20	M			189	285	Mexico	Bautista-Cruz and del Castillo 2005
Mature	20	M			106	160	Brazil	Smith et al. 1998
Mature	20	M			210	317	Mexico	Bautista-Cruz and del Castillo 2005
Mature	20	M			126	190	Mexico	Bautista-Cruz and del Castillo 2005
Mature	30	M			70	86	Puerto Rico	Marin-Spiotta 2006
Mature	30	M			44	54	Puerto Rico	Marin-Spiotta 2006

(continued)

Appendix 2.2 (continued)

Age (y)	Depth (cm)	Life Zone	Past Land Use	Cover type	Soil C (Mg/ha)	Soil C 0–25 cm (Mg/ha)	Location	Reference
Mature	30	M			73	89	Puerto Rico	Marin-Spiotta 2006
Mature	40	M			57	60	Brazil	Sommer et al. 2000
Mature	5	W			29	112	Ecuador	Fehse et al. 2002
Mature	10	W			14	30	Costa Rica	Reiners et al. 1994
Mature	10	W			17	37	Costa Rica	Reiners et al. 1994
Mature	10	W			28	60	Costa Rica	Reiners et al. 1994
Mature	20	W			23	28	Brazil	Johnson et al. 2001
Mature	25	W			89	89	USA-Hawaii	Bashkin and Binkley 1998
Mature	25	W			110	110	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
Mature	25	W			85	85	Puerto Rico and US Virgin Islands	Brown and Lugo 1990b
Mature	25	W			62	62	Puerto Rico	Lugo et al. 1986
Mature	30	W			87	75	Costa Rica	Guariguata et al. 1997
Mature	30	W			91	78	Costa Rica	Guariguata et al. 1997
Mature	30	W			116	100	Costa Rica	Guariguata et al. 1997
Mature	30	W			90	77	Ecuador	Rhoades et al. 2000
Mature	30	W			109	94	Ecuador	Rhoades et al. 2000
Mature	30	W			49	42	Costa Rica	Werner 1984

References

Achard, F., Eva, H. D., Stibig, H.-J., Mayaux, P., Gallego, J., Richards, T., and Malingreau, J.-P. 2002. Determination of deforestation rates of the world's humid tropical forests. Science 297:999–1002.

Adachi, M., Bekku, Y. S., Rashidah, W., Okuda, T., and Koizumi, H. 2006. Differences in soil respiration between different tropical ecosystems. Applied Soil Ecology 34:258–265.

Ahmad, R., Kookana, R. S., Alston, A. M., and Skjemstad, J. O. 2001. The nature of soil organic matter affects sorption of pesticides. 1. Relationships with carbon chemistry as determined by ^{13}C CPMAS NMR spectroscopy. Environment, Science and Technology 35:878–884.

Aide, T. M., Zimmerman, J. K., Herrera, L., Rosario, M., and Serrano, M. 1995. Forest recovery in abandoned tropical pastures in Puerto Rico. Forest Ecology and Management 77:77–86.

Aide, T. M., Zimmerman, J. K., Pascarella, J. B., Rivera, L., and Marcano-Vega, H. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. Restoration Ecology 8:328–338.

Aide, T. M., and Grau, H. R. 2004. Globalization, migration, and Latin American ecosystems. Science 305:1915–1916.

Alvarez, C. R., Alvarez, R., Grigera, M. S., and Lavado, R. S. 1998. Associations between organic matter fractions and the active soil microbial biomass. Soil Biology and Biochemistry 30:767–773.

Alves, D. S., Vianei Soares, J., Amaral, S., Mello, E. M. K., Almeida, S. A. S., Fernandes da Silva, O., and Silveira, A. M. 1997. Biomass of primary and secondary vegetation in Rondônia, Western Brazilian Amazon. Global Change Biology 3:451–461.

Amundson, R. 2001. The carbon budget in soils. Annual Review of Earth and Planetary Science 29:535–562.

Anderson, K. J., Allen, A. P., Gillooly, J. F., and Brown, J. H. 2006. Temperature-dependence of biomass accumulation rates during secondary succession. Ecology Letters 9:673–682.

Arroyo-Mora, J. P., Sánchez-Azofeifa, G. A., Rivard, B., Calvo, J. C., and Janzen, D. H. 2005. Dynamics in landscape structure and composition for the Chorotega region, Costa Rica from 1960 to 2000. Agriculture, Ecosystems and Environment 106:27–39.

Baisden, W. T., Amundson, R., Cook, A. C., and Brenner, D. L. 2002. Turnover and storage of C and N in five density fractions from California annual grassland surface soils. Global Biogeochemical Cycles 16:117, doi:10.1029/2001GB001822,2002

Balabane, M., Faivre, D., van Oort, F., and Dahmani-Muller, H. 1999. Mutual effects of soil organic matter dynamics and heavy metals fate in a metallophyte grassland. Environmental Pollution 105:45–54.

Baldock, J. A., Masiello, C. A., Gélinas, Y., and Hedges, J. I. 2004. Cycling and composition of organic matter in terrestrial and marine ecosystems. Marine Chemistry 92:39–64.

Balesdent, J., Mariotti, A., and Guillet, B. 1987. Natural ^{13}C abundance as a tracer for studies of soil organic matter dynamics. Soil Biology and Biochemistry 19:25–30.

Bashkin, M.A., and Binkley, D. 1998. Changes in soil carbon following afforestation in Hawaii. Ecology 79:828–833.

Bautista-Cruz, A., and del Castillo, R. F. 2005. Soil changes during secondary succession in a tropical montane cloud forest area. Soil Science Society of America Journal 69:906–914.

Bernoux, M., Cerri, C. C., Neill, C., and de Moraes, J. F. L. 1998. The use of stable carbon isotopes for estimating soil organic matter turnover rates. Geoderma 82:43–58.

Binkley, D. and Resh, S. C. 1999. Rapid changes in soils following Eucalyptus afforestation in Hawaii. Soil Science Society of America Journal 63:222–225.

Binkley, D., Kaye, J., Barry, M., and Ryan, M. G. 2004. First-rotation changes in soil carbon and nitrogen in a Eucalyptus plantation in Hawaii. Soil Science Society of America Journal 68:1713–1719.

Bird, J. A., van Kessel, C., and Horwarth, W. R. 2003. Stabilization of ^{13}C-Carbon and immobilization of ^{15}N-Nitrogen from rice straw in humic fractions. Soil Science Society of America Journal 67:806–816.

Boucher, D. H., Vandermeer, J. H., Granzow de la Cerda, I., Mallona, M. A., Perfecto, I., and Zamora, N. 2000. Post-agriculture versus post-hurricane succession in southeastern Nicaraguan rain forest. Plant Ecology 156:131–137.

Brady, N. C., and Weil, R. R., Eds. 2002. The Nature and Properties of Soils, 13th edition. New Jersey: Prentice Hall.

Brandeis, T. J., and Suárez Rozo, M. de R. 2005. Effects of model choice and forest structure on inventory-based estimations of Puerto Rican forest biomass. Caribbean Journal of Science 41:250–268.

Brown, S., and Lugo, A. E. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. Biotropica 14:161–187.

Brown, S., and Lugo, A. E. 1984. Biomass of tropical forests: a new estimate based on forest volumes. Science 223:1290–1293.

Brown, S., Gillespie, A. J. R., and Lugo, A. E. 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. Forest Science 35:881–902.

Brown, S., and Lugo, A. E. 1990. Tropical secondary forests. Journal of Tropical Ecology 6:1–32.

Brown, S., Sathaye, J., Cannell, M., and Kauppi, P., et al. 1995a. Management of forests for mitigation of greenhouse gas emissions. In Climate Change 1995: Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses. Working Group II to Second Assessment Report of the Intergovernmental Panel on Climate Change, ed. R. T. Watson, M. C. Zinyowera, and R. H. Moss, pp. 775–797. New York: Cambridge University Press.

Brown, I. F., Martinelli, L. A., Thomas, W. W., Moreira, M. Z., Cid Ferreira, C. A., and Victoria, R. A. 1995b. Uncertainty in the biomass of Amazonian forests: an example from Rondônia, Brazil. Forest Ecology and Management 75:175–189.

Bunker, D. E., DeClerck, F., Bradford, J. C., Colwell, R. K., Perfecto, I., Phillips, O. L., Sankaran, M., and Naeem, S. 2005. Species loss and aboveground carbon storage in a tropical forest. Science 310:1029–1031.

Buschbacher, R. 1986. Tropical deforestation and pasture development. Bioscience 36:23–27.

Buschbacher, R., Uhl, C., and Serrão, E.A. S. 1988. Abandoned pastures in Eastern Amazonia. II. Nutrient stocks in the soil and vegetation. Journal of Ecology 76: 682–699.

Bush, M. B., and Colinvaux, P. A. 1994. Tropical forest disturbance: paleoecological records from Darien, Panama. Ecology 75:1761–1768.

Byers, S. C., Mills, E. L., and Stewart, P. L. 1978. A comparison of methods of determining organic carbon in marine sediments, with suggestions for a standard method. Hydrobiologia 58:43–47.

Cambardella, C., and Elliott, E. T. 1993. Carbon and nitrogen distribution in aggregates form cultivated and native grassland soils. Soil Science Society of America Journal 57:1071–1076.

Capers, R. S., Chazdon, R. L., Redondo Brenes, A., and Vilchez Alvarado, B. 2005. Successional dynamics of woody seedling communities in wet tropical secondary forests. Journal of Ecology 93:1071–1084.

Carpenter, F. L., Palacios Mayorga, S., González Quintero, E., and Schroeder, M. 2001. Land-use and erosion of a Costa Rican Ultisol affect soil chemistry, mycorrhizal fungi and early regeneration. Forest Ecology and Management 144:1–17.

Carvalheiro, K. D. O., and Nepstad, D. C. 1996. Deep soil heterogeneity and fine root distribution in forests and pastures of eastern Amazônia. Plant and Soil 182:279–285.

Caspersen, J. P., Pacala, S. W., Jenkins, J. C., Hurtt, G. C., Moorcroft, P. R., and Birdsey, R. A. 2000. Contributions of land-use history to carbon accumulation in U.S. forests. Science 290:1148–1151.

Chambers, J. Q., Higuchi, N., and Schimel, J. P. 1998. Ancient trees in Amazônia. Nature 391: 135–136.

Chambers, J. Q., dos Santos, J., Ribeiro, R. J., and Higuchi, N. 2001. Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. Forest Ecology and Management 152:73–84.

Chazdon, R. L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. Perspectives in Plant Ecology, Evolution and Systematics 6:51–71.

Chin, Y.-P., Aiken, G., and O'Loughlin, E. 1994. Molecular weight, polydispersity, and spectroscopic properties of aquatic humic substances. Environment, Science and Technology 28:1853–1858.

Christensen, B. T. 2001. Physical fractionation of soil and structural and functional complexity in organic matter turnover. European Journal of Soil Science 52:345–353.

Clark, D. B., and Clark, D. A. 1991. The impact of physical damage on canopy tree regeneration in tropical rain forest. Journal of Ecology 79:447–457.

Clark, D. B., Clark, D. A., Brown, S., Oberbauer, S. F., and Veldkamp, E. 2002. Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. Forest Ecology and Management 164:237–248.

Clark, D. A., Pipers, S. C., Keeling, C. D., and Clark, D. B. 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. Proceedings of the National Academy of Sciences 100:5852–5857.

Compton, J. E., and Boone, R. D. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology 81:2314–2330.

Croué, J.-P. 2004. Isolation of humic and non-humic NOM fractions: structural characterization. Environmental Monitoring and Assessment 92:193–207.

Crowther, J. 1980. Soil carbon dioxide and weathering potentials in tropical karst terrain, peninsular Malaysia: a preliminary model. Earth Surface Processes and Landforms 9:397–407.

Cuevas, E., Brown, S., and Lugo, A. E. 1991. Above- and belowground organic matter storage and production in a tropical pine plantation and a paired broadleaf secondary forest. Plant and soil 135:257–268.

Cusack, D., and Montagnini, F. 2004. The role of native species plantations in recovery of understory woody diversity in degraded pasturelands of Costa Rica. Forest Ecology and Management 188:1–15.

Davidson, E. A., de Carvalho, C. J. R., Vieira, I. C. G., Figuereido, R. de O., Moutinho, P., Ishida, F. Y., dos Santos, M. T. P., Guerrero, J. B., Kalif, K., and Saba, R. T. 2004. Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. Ecological Applications 14:S150–S163.

de Camargo, P. S., Trumbore, S. E., Martinelli, L. A., Davidson, E. A., Nepstad, D. C., and Victoria, R. L. 1999. Soil carbon dynamics in regrowing forest of eastern Amazônia. Global Change Biology 5:693–702.

de Jong, W., Chokkalingam, U., and Perrera, G. A. D. 2001. The evolution of swidden fallow secondary forests in Asia. Journal of Tropical Forest Science 13:800–814.

de Koning, G. H. J., Veldkamp, E., and López-Ulloa, M. 2003. Quantification of carbon sequestration in soils following pasture to forest conversion in northwestern Ecuador. Global Biogeochemical Cycles 17:1098, doi:10.1029/2003GB002099.

Dean, W. E. 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. Journal of Sedimentary Petrology 44:242–248.

DeFries, R. S., Houghton, R. A., Hansen, M. C., Field, C. B., Skole, D., and Townsend, J. 2002. Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 1990s. Proceedings of the National Academy of Sciences 99:14256–14261.

Delaney, M., Brown, S., Lugo, A. E., Torrez-Lezama, A., and Bello Quintero, N. 1997. The distribution of organic carbon in major components of forests located in five life zones of Venezuela. Journal of Tropical Ecology 13:697–708.

Delaney, M., Brown, S., Lugo, A.E., Torrez-Lezama, A., and Bello Quintero, N., 1998. The quantity and turnover of dead wood in permanent forest plots in six life gones of Venezuela. Biotropica 30:2–11.

Denslow, J. S., and Guzmán, S. G. 2000. Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. Journal of Vegetation Science 11:201–212.

DeWalt, S. J., Maliakal, S. K., and Denslow, J. S. 2003. Changes in vegetation structure and composition along a tropical forest chronosequence: implications for wildlife. Forest Ecology and Management 182:139–151.

Dietz, J. L. 1986. Economic History of Puerto Rico: Institutional Change and Capitalist Development. Princeton, NJ: Princeton University Press.

Dixon, R. K., Brown, S., Houghton, R. A., Solomon, A. M., Trexler, M. C., and Wisniewski, J. 1994. Carbon pools and flux of global forest ecosystems. Science 263:185–190.

Drake, D. R., and Pratt, L. W. 2001. Seedling mortality in Hawaiian rain forest: the toll of small-scale physical disturbance. Biotropica 33: 319–323.

Dunn, R. R. 2004. Recovery of faunal communities during tropical forest regeneration. Conservation Biology 18:302–309.

Eaton, J. M., and Lawrence, D. 2006. Woody debris stocks and fluxes during succession. Forest Ecology and Management 232:46–55.

Elliott, E. T., and Cambardella, C. A. 1991. Physical separation of soil organic matter. Agriculture, Ecosystems and Environment 34:407–419.

Eswaran, H., van den Berg, E., and Reich, P. 1993. Organic carbon in soils of the world. Soil Science Society of America Journal 57:192–194.

Etter, A., McAlpine, C., Pullar, D., and Possingham, H. 2005. Modeling the age of tropical moist forest fragments in heavily-cleared lowland landscapes of Colombia. Forest Ecology and Management 208:249–260.

Eva, H. D., Achard, F., Stibig, H.-J., and Mayaux, P. 2003. Response to Comment on "Determination of deforestation rates of the world's humid tropical forests". Science 299:1015b.

Ewel, J. J. 1976. Litterfall and leaf decomposition in a tropical forest succession in eastern Guatemala. The Journal of Ecology 64:293–308.

Farenhorst, A. 2006. Importance of soil organic matter fractions in soil-landscape and regional assessment of pesticide sorption and leaching in soil. Soil Science Society of America Journal 70:1005–1012.

Farquhar, G. D., Ehleringer, J.R., and Hubick, K.T. 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology 40:503–537.

Fearnside, P. M. 1993. Deforestation in Brazilian Amazon: The effect of population land tenure. Ambio 22:537–545.

Fearnside, P. M. 1996. Amazonian deforestation and global warming: carbon stocks in vegetation replacing Brazil's Amazon forest. Forest Ecology and Management 80:21–34.

Fearnside, P. M., and Guimarães, W. M. 1996. Carbon uptake by secondary forests in Brazilian Amazônia. Forest Ecology and Management 80:35–46.

Fearnside, P. M., and Laurance, W. F. 2003. Comment on "Determination of deforestation rates of the world's humid tropical forests". Science 299:1015a.

Fehse, J., Hofstede, R., Aguirre, N., Paladines, C., Kooijman, A., and Sevnik, J. 2002. High altitude tropical secondary forests: a competitive carbon sink? Forest Ecology and Management 163:9–25.

Feldpausch, T. R., Rondon, M. A., Fernandes, E. C. M., Riha, S. J., and Wandelli, E. 2004. Carbon and nutrient accumulation in secondary forests regenerating on pastures in Central Amazônia. Ecological Applications 14:164–176.

Fichtler, E., Clark, D. A., and Worbes, M. 2003. Age and long-term growth of trees in an old-growth tropical rain forest, based on analyses of tree rings and ^{14}C. Biotropica 35:306–317.

Fisher, M. J., Rao, I. M., Ayarza, M. A., Lascano, C. E., Sanz, J. I., Thomas, R. J., and Vera, R. R. 1994. Carbon storage by introduced deep-rooted grasses in South African savannas. Nature 371:236–238.

Fölster, H., De Las Salas, G., and Khanna, P. 1976. A tropical evergreen forest site with perched water table, Magdalena Valley, Columbia: biomass and bioelement inventory of primary and secondary vegetation. Oecologia Planetarium 11:297–320.

Gehring, C., Denich, M., Kanashiro, M., and Vlek, P. L. G. 1999. Response of secondary vegetation in Eastern Amazônia to relaxed nutrient availability constraints. Biogeochemistry 45:223–241.

Gehring, C., Denich, M., and Vlek, P. L. G. 2005. Resiliency of secondary forest regrowth after slash-and-burn agriculture in central Amazonia. Journal of Tropical Ecology 21:519–527.

Gerwing, J. J., and Lopes Farias, D. 2000. Integrating liana abundance and forest structure into an estimate of total aboveground biomass for an eastern Amazonian forest. Journal of Tropical Ecology 16:327–335.

Gibbard, S. G., Caldeira, K., Bala, G., Phillips, T., and Wickett, M. 2005. Climate effects of global land cover change. Geophysical Research Letters 32.

Gillman, L. N., Ogden, J., Wright, S. D., Stewart, K. L., and Walsh, D. P. 2004. The influence of macro-litterfall and forest structure on litterfall damage to seedlings. Austral Ecology 29:305–312.

Gleixner, G., Bol, R., and Balesdent, J. 1999. Molecular insight into soil carbon turnover. Rapid Communications in Mass Spectrometry 13:1278–1283.

Golchin, A., Oades, J. M., Skjemstad, J. O., and Clarke, P. 1994. Study of free and occluded particulate organic matter in soils by solid state ^{13}C CP/MAS NMR spectroscopy and scanning electron microscopy. Soil Biology and Biochemistry 32:285–309.

Golchin, A., Oades, J. M., Skjemstad, J. O., and Clarke, P. 1995. Structural and dynamic properties of soil organic matter as reflected by ^{13}C natural abundance, pyrolysis mass spectrometry and solid-state ^{13}C NMR spectroscopy in density fractions of an Oxisol under forest and pasture. Australian Journal of Soil Research 33:59–76.

Grau, H. R., Aide, T. M., Zimmerman, J. K., and Thomlinson, J. R. 2004. Trends and scenarios of the carbon budget in postagricultural Puerto Rico (1936–2060). Global Change Biology 10:1163–1179.

Greenland, D. J., and Ford, G. W. 1964. Separation of partially humified organic materials by ultrasonic dispersion. Pages 137–148 in 8th International Congress of Soil Science, Transactions.

Guariguata, M. R., Chazdon, R. L., Denslow, J. S., Dupuy, J. M., and Anderson, L. 1997. Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. Plant Ecology 132:107–120.

Guariguata, M. R. 1998. Response of forest tree saplings to experimental mechanical damage in lowland Panama. Forest Ecology and Management 102:103–111.

Guariguata, M. R., and Ostertag, R. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. Forest Ecology and Management 5292:1–22.

Guggenberger, G., Zech, W., and Thomas, R. J. 1995a. Lignin and carbohydrate alteration in particle-size separates of an Oxisol under tropical pastures following native savanna. Soil Biology and Biochemistry 27:1629–1638.

Guggenberger, G., Zech, W., Haumaier, L., and Christensen, B. T. 1995b. Land-use effects on the composition of organic matter in particle-size separates of soils: II. CPMAS and solution ^{13}C NMR analysis. European Journal of Soil Science 46:147–158.

Guggenberger, G., and Zech, W. 1999. Soil organic matter composition under primary forest, pasture, and secondary forest succession, Region Huetar Norte, Costa Rica. Forest Ecology and Management 124:93–104.

Hanson, P. J., Swanston, C. W., Garten Jr., C. T., Todd, D. E., and Trumbore, S. E. 2005. Reconciling change in Oi-horizon carbon-14 with mass loss for an oak forest. Soil Science Society of America Journal 69:1492–1502.

Harmon, M. E., Whigham, D. F., Sexton, J., and Olmsted, I. 1995. Decomposition and mass of woody detritus in the dry tropical forests of the Northeastern Yucatan Peninsula, Mexico. Biotropica 27:305–316.

Harmon, M. E., and Sexton, J. 1996. Guidelines for the measurements of woody debris in forest ecosystems. U.S. LTER Publication no. 20.

Hecht, S. B. 2005. Soybeans, development and conservation on the Amazon frontier. Development and Change 36:375–404.

Helfrich, M., Ludwig, B., Buurman, P., and Flessa, H. 2006. Effect of land use on the composition of soil organic matter in density and aggregate fractions as revealed by solid-state ^{13}C NMR spectroscopy. Geoderma 136:331–341.

Helmer, E. H., Brown, S., and Cohen, W. B. 2000. Mapping montane tropical forest successional stage and land use with multi-date Landsat imagery. International Journal of Remote Sensing 21:2163–2183.

Helmer, E. H. 2004. Forest conservation and land development in Puerto Rico. Landscape Ecology 19:29–40.

Hertel, D., Leuschner, C., and Hoelscher, D. 2003. Size and structure of fine root systems in old-growth and secondary tropical montane forests (Costa Rica). Biotropica 35:143–153.

Holl, K. D. 1998. Do bird perching structures elevate see rain and seedling establishment in abandoned tropical pasture? Restoration Ecology 6:227–313.

Holl, K. D. 1999. Tropical forest recovery and restoration. Trends in Ecology and Evolution 14:378–379.

Holl, K. D., Loik, M. E., Lin, E. H. V., and Samuels, I. A. 2000. Tropical montane forest restoration in Costa Rica: Overcoming barriers to dispersal and establishment. Restoration Ecology 8:339–349.

Houghton, R. A., Skole, D. L., and Lefkowitz, D. S. 1991. Changes in the landscape of Latin America between 1850 and 1985. II. Net release of CO_2 to the atmosphere. Forest Ecology and Management 38:173–199.

Houghton, R. A., Skole, D. L., Nobre, C. A., Hackler, J. L., Lawrence, K. T., and Chomentowski, W. H. 2000. Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon. Nature 403:301–303.

Houghton, R. A., and Goodale, C. L. 2004. Effects of land-use change on the carbon balance of terrestrial ecosystems. Ecosystems and Land Use Change. Geophysical Monograph Series 153:85–98.

Hughes, R. F., Kauffman, J. B., and Jaramillo, V. J. 1999. Biomass, carbon and nutrient dynamics of secondary forests in a humid tropical region of Mexico. Ecology 80:1892–1907.

Hughes, R. F., Kauffman, J. B., and Cummings, D. L. 2000a. Fire in the Brazilian Amazon. 3. Dynamics of biomass, C, and nutrient pools in regenerating forests. Oecologia 124: 574–588.

Hughes, R. F., Kauffman, J. B., and Jaramillo, V. J. 2000b. Ecosystem-scale impacts of deforestation and land use in a humid tropical region of Mexico. Ecological Applications 10:515–527.

Janisch, J. E., and Harmon, M. E. 2002. Successional changes in live and dead wood carbon stores: Implications for net ecosystem productivity. Tree Physiology 22:77–89.

Jaramillo, V. J., Ahedo-Hernandez, R., and Kauffman, J. B. 2003. Root biomass and carbon in a tropical evergreen forest of Mexico: Changes with secondary succession and forest conversion to pasture. Journal of Tropical Ecology 19:457–464.

Jenkinson, D. S., and Rayner, J. H. 1977. The turnover of soil organic matter in some of the Rothamsted classical experiments. Soil Science 123:298–304.

Jobbágy, E. G., and Jackson, R. B. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications 10:423–436.

John, B., Yamashita, T., Ludwig, B., and Flessa, H. 2005. Storage of organic carbon in aggregate and density fractions of silty soils under different land uses. Geoderma 128:63–79.

Johnson, C. M., Zarin, D. J., and Johnson, A. H. 2000. Post-disturbance aboveground biomass accumulation in global secondary forests. Ecology 81:1395–1401.

Johnson, C. M., Vieira, I. C. G., Zarin, D. J., Frizano, J., and Johnson, A. H. 2001. Carbon and nutrient storage in primary and secondary forests in eastern Amazônia. Forest Ecology and Management 147:245–252.

Jordan, C. F., and Farnworth, E. G. 1982. Natural vs. plantation forests: a case study of land reclamation strategies for the humid tropics. Environmental Management 6:485–492.

Kammesheidt, L. 2002. Perspectives on secondary forest management in tropical humid lowland America. Ambio 31:243–250.

Kaye, J. P., Resh, S. C., Kaye, M. W, and Chimner, R. A. 2000. Nutrient and carbon dynamics in a replacement series of Eucalyptus and Albizia trees. Ecology 81:3267–3273.

Keller, M., Palace, M., and Hurtt, G. 2001. Biomass estimation in the Tapajos National Forest, Brazil. Examination of sampling and allometric uncertainties. Forest Ecology and Management 154:371–382.

Keller, M., Palace, M, Asner, G. P., Pereira Jr., R., and Silva, J. N. M. 2004. Coarse woody debris in undisturbed and logged forests in the eastern Brazilian Amazon. Global Change Biology 10:784–795.

Kennard, D. K. 2002. Secondary forest succession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia. Journal of Tropical Ecology 18:53–66.

Kögel-Knabner, I. 2000. Analytical approaches for characterizing soil organic matter. Organic Geochemistry 31:609–625.

Kraenzel, M., Castillo, A., Moore, T., and Potvin, C. 2003. Carbon storage of harvest-age teak (Tectona grandis) plantations, Panama. Forest Ecology and Management 173:213–225.

Krull, E. S., Baldock, J. A., and Skjemstad, J. O. 2003. Importance of mechanisms and processes of the stabilisation of soil organic matter for modelling carbon turnover. Functional Plant Biology 30:207–222.

Lawrence, D. 2005a. Biomass accumulation after 10–200 years of shifting cultivation in Bornean rain forest. Ecology 86:26–33.

Lawrence, D. 2005b. Regional-scale variation in litter production and seasonality in tropical dry forests of southern Mexico. Biotropica 37:561–570.

Lemenih, M., Olsson, M., and Karltun, E. 2004. Comparison of soil attributes under Cupressus lusitanica and Eucalyptus saligna established on abandoned farmlands with continuously cropped farmlands and natural forest in Ethiopia. Forest Ecology and Management 195:57–67.

Li, Y., Xu, M., Zou, X., Shi, P., and Zhang,Y. 2005. Comparing soil organic carbon dynamics in plantation and secondary forest in wet tropics in Puerto Rico. Global Change Biology 11:239–248.

Losi, C. J., Siccama, T. G., Condit, R., and Morales, J. E. 2003. Analysis of alternative methods for estimating carbon stock in young tropical plantations. Forest Ecology and Management 184:355–368.

López-Ulloa, M., Veldkamp, E., and de Koning, G. H. J. 2005. Soil carbon stabilization in converted tropical pastures and forests depends on soil type. Soil Science Society of America Journal 69:1110–1117.

Louchouarn, P., Opsahl, S., and Benner, R. 2000. Isolation and quantification of dissolved lignin from natural waters using solid-phase extraction and GC/MS. Analytical Chemistry 72:2780–2787.

Lovley, D. R., Coates, J. D., Blunt-Harris, E. L., Phillips, E. J. P., and Woodward, J. C. 1996. Humic substances as electron acceptors for microbial respiration. Nature 382:445–448.

Lucas, R. M., Honzak, M., do Amaral, I., Curran, P. J., and Foody, G. M. 2002. Forest regeneration on abandoned clearances in central Amazônia. International Journal of Remote Sensing 23:965–988.

Lugo, A. E. 1988. The future of the forest. Ecosystem rehabilitation in the tropics. Environment 30:17–20, 41–45.

Lugo, A. E. 1992. Comparison of tropical tree plantations with secondary forests of similar age. Ecological Monographs 62:1–41.

Lugo, A. E., Brown, S., and Chapman, J., 1988. An analytical review of production rates and stemwood biomass of tropical forests plantations. Forest Ecology and Management 23: 179–200.

Lugo, A. E., and Helmer, E. 2004. Emerging forests on abandoned land: Puerto Rico's new forests. Forest Ecology and Management 190:145–161.

Makana, J.-R., and Thomas, S. C. 2006. Impacts of selective logging and agricultural clearing on forest structure, floristic composition and diversity, and timber tree regeneration in the Ituri Forest, Democratic Republic of Congo. Biodiversity and Conservation 15:1375–1397.

Malhi, Y., Baldocchi, D. D., and Jarvis, P. G. 1999. The carbon balance of tropical, temperate and boreal forests. Plant, Cell and Environment 22:715–740.

Mann, L. K. 1986. Changes in soil carbon storage after cultivation. Soil Science 142:279–288.

Marcano-Vega, H., Aide, T. M., and Baez, D. 2002. Forest regeneration in abandoned coffee plantations and pastures in the Cordillera Central of Puerto Rico. Plant Ecology 161:75–87.

Marín-Spiotta, E. 2006. Controls on above and belowground carbon storage during tropical reforestation. PhD Thesis. University of California, Berkeley.

Marín-Spiotta, E., Ostertag, R., and Silver, W. L. 2007. Long-term patterns in tropical reforestation: plant community composition and aboveground biomass accumulation. Ecological Applications 17:828–839.

Marrero, J. 1950. Reforestation of degraded lands in Puerto Rico. Caribbean Forester 11:3–15.

Martin, A., Mariotti, A., Balesdent, J., Lavelle, P., and Vuattoux, R. 1990. Estimate of organic matter turnover rate in a savanna soil by ^{13}C natural abundance measurements. Soil Biology and Biochemistry 22:517–523.

Maury-Lechon, G. 1982. Regeneration forestière en Guyana française: recru sur 25 ha de coupe papetière en forêt dense humide (Arbocel.). Revue Boiset Forêts des Tropiques 197:3–21.

McDonald, M. A., and Healey, J. R. 2000. Nutrient cycling in secondary forests in the Blue Mountains of Jamaica. Forest Ecology and Management 139:257–278.

McGroddy, M., and Silver, W. L. 2000. Variations in belowground carbon storage and soil CO_2 flux rates along a wet tropical climate gradient. Biotropica 32:614–624.

McWilliam, A. L. C., Robertos, J. M., Cabral, O. M. R., Leitão, M. V. B. R., de Costa, A. C. L., Maitelli, G. T., and Zamparoni, C. A. G. P. 1993. Leaf area index and above-ground biomass of terra firme rain forest and adjacent clearings in Amazonia. Functional Ecology 7:310–317.

Metz, B., Davidson, O., Swart, R., and Pan, J. 2001. Climate Change 2001. Mitigation. Contribution of Working Group III to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge: Cambridge University Press.

Mikutta, R., Kleber, M., Torn, M. S., and Jahn, R. 2006. Stabilization of soil organic matter: association with minerals or chemical recalcitrance? Biogeochemistry 77:25–56.

Mizrahi, A., Ramos Prado, J. M., and Jimenez-Osornio, J. 1997. Composition, structure, and management potential of secondary dry tropical vegetation in two abandoned henequen plantations of Yucatan, Mexico. Forest Ecology and Management 96:273–282.

Murphy, P. G., and Lugo, A. E. 1995. Dry forests of Central America and the Caribbean. In Seasonally Dry Tropical Forests, ed. S. H. Bullock, H. A. Mooney, and E. Medina, pp. 9–34. United Kingdom: Cambridge University Press.

Myster, R. W. 2004. Post-agricultural invasion, establishment, and growth of neotropical trees. The Botanical Review 70:381–402.

Naughton-Treves, L., and Chapman, C. A. 2002. Fuelwood resources and forest regeneration on fallow land in Uganda. Journal of Sustainable Forestry 14:19–32.

Neeff, T. 2005. Spatial modeling of primary and secondary forest growth in Amazonia. Forest Ecology and Management 219:149–168.

Neeff, T., Lucas, R. M., dos Santos, J. R., Brondizio, E. S., and Freitas, C. C. 2006. Area and age of secondary forests in Brazilian Amazônia 1978–2002: an empirical estimate. Ecosystems 9:609–623.

Neff, J. C., Townsend, A. R., Gleixner, G., Lehman, S. J., Turnbull, J., and Bowman, W. D. 2002. Variable effects of nitrogen additions on the stability and turnover of soil carbon. Nature 419:915–917.

Neill, C., Melillo, J. M., Steudler, P. A., Cerri, C. C., de Moraes, J. F. L., Piccolo, M. C., and Brito, M. 1997. Soil carbon and nitrogen stocks following forest clearing for pasture in the southwestern Brazilian Amazon. Ecological Applications 7:1216–1225.

Nelson, D. W., and Sommers, L. E. 1996. Total carbon, organic carbon, and organic matter. In Methods of soil analysis Part 3, ed. D. L. Sparks, pp. 961–1010. Madison, WI: Soil Science Society of America.

Nepstad, D. C., Uhl, C., and Serrão, E. A. S. 1991. Recuperation of a degraded Amazonian landscape: forest recovery and agricultural restoration. Ambio 20:248–255.

Nepstad, D. C., de Carvalho, C. R., Davidson, E. A., Jipp, P. H., Lefebvre, P. A., Negreiros, G. H., da Silva, E. D., Stone, T. A., Trumbore, S. E., and Vieira, S. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature 372: 666–669.

Nepstad, D. C., Stickler, C. M., and Almeida, O. T. 2006. Globalization of the Amazon soy and beef industries: opportunities for conservation. Conservation Biology 20:1595–1603.

Neufeldt, H., Resck, D. V. S., and Ayarza, M. A. 2002. Texture and land-use effects on soil organic matter in Cerrado Oxisols, Central Brazil. Geoderma 107:151–164.

Nierop, K. G. J., Pulleman, M. M., and Marinissen, J. C. Y. 2001. Management induced organic matter differentiation in grassland and arable soil: a study using pyrolysis techniques. Soil Biology and Biochemistry 33:755–764.

Northcott, G. L. and Jones, K. C. 2000. Experimental approaches and analytical techniques for determining organic compound bound residues in soil and sediment. Environmental Pollution 108:19–43.

Oades, J. M. 1988. The retention of organic matter in soils. Biogeochemistry 5:35–70.

Oades, J. M., Waters, A. G., Vassallo, A. M., Wilson, M. A., and Jones, G. P. 1988. Influence of management on the composition of organic matter in a red-brown earth as shown by ^{13}C nuclear magnetic resonance. Australian Journal of Soil Research 26:289–299.

Oliver, C., and Larson, B. 1996. Forest Stand Dynamics. New York: John Wiley and Sons.

Paniagua, A., Kammerbauer, J., Avedillo, M., and Andrews, A. M. 1999. Relationship of soil characteristics to vegetation successions on a sequence of degraded and rehabilitated soils in Honduras. Agriculture, Ecosystems and Environment 72:215–225.

Parrotta, J. A., and Knowles, O. H. 1999. Restoration of tropical moist forests on bauxite-mined lands in the Brazilian Amazon. Restoration Ecology 7:103–116.

Parton, W. J., Schimel, D. S., Cole, C. V., and Ojima, D. S. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal 51:1173–1179.

Pascarella, J. B., Aide, T. M., and Zimmerman, J. K. 2004. Short-term response of secondary forests to hurricane disturbance in Puerto Rico, USA. Forest Ecology and Management 199:379–393.

Paul, E. A. 1984. Dynamics of organic matter in soils. Plant and soil 76:275–285.

Paul, K. I., Polglase, P. J., Nyakuengama, J. G., and Khanna, P. K. 2002. Change in soil carbon following afforestation. Forest Ecology and Management 168:241–257.

Paul, E. A., Morris, S. J., Conant, R. T., and Plante, A. F. 2006. Does the acid hydrolysis-incubation method measure meaningful soil organic carbon pools? Soil Science Society of America Journal 70:1023–1035.

Peña-Claros, M. 2003. Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. Biotropica 35:450–461.

Poirier, N., Sohi, S. P., Gaunt, J. L., Mahieu, N., Randall, E. W., Powlson, D. S., and Evershed, R. P. 2005. The chemical composition of measurable soil organic matter pools. Organic Geochemistry 36:1174–1189.

Post, W. M., Emanuel, W. R., Zinke, P. J., and Stangenberger, A. G. 1982. Soil carbon pools and world life zones. Nature 298:156–159.

Post, W. M., and Kwon, K. C. 2000. Soil carbon sequestration and land-use change: processes and potential. Global Change Biology 6:317–327.

Potvin, C., Whidden, E., and Moore, T. 2004. A case study of carbon pools under three different land-uses in Panama. Climatic Change 67:291–307.

Powers, J. S. 2004. Changes in soil carbon and nitrogen after contrasting land-use transitions in northeastern Costa Rica. Ecosystems 7:134–146.

Powers, J. S., Read, J. M., Denslow, J. S., and Guzman, S. M. 2004. Estimating soil carbon fluxes following land-cover change: a test of some critical assumptions for a region in Costa Rica. Global Change Biology 10:170–181.

Pregitzer, K. S., and Euskirchen, E. S. 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. Global Change Biology 10:1–26.

Preston, C. M. 2001. Carbon-13 solid-state NMR of soil organic matter - using the technique effectively. Canadian Journal of Soil Science 81:255–270.

Ramakrishnan, P. S., and Toky, O. 1983. Secondary succession following slash and burn agriculture in Northeastern India. 2. Nutrient cycling. Journal of Ecology 71:747–758.

Rasiah, V., Florentine, S. K., Williams, B. L., and Westbrooke, M. E. 2004. The impact of deforestation and pasture abandonment on soil properties in the wet tropics of Australia. Geoderma 120:35–45.

Read, L., and Lawrence, D. 2003a. Recovery of biomass following shifting cultivation in dry tropical forests of the Yucatan. Ecological Applications 13:85–97.

Read, L., and Lawrence, D. 2003b. Litter nutrient dynamics during succession in dry tropical forests of the Yucatan: regional and seasonal effects. Ecosystems 6:747–761.

Redondo-Brenes, A., and Montagnini, F. 2006. Growth, productivity, aboveground biomass, and carbon sequestration of pure and mixed native tree plantations in the Caribbean lowlands of Costa Rica. Forest Ecology and Management 232:168–178.

Reiners, W. A., Bouwman, A. F., Parsons, W. J. F., and Keller, M. 1994. Tropical rain forest conversion to pasture: changes in vegetation and soil properties. Ecological Applications 4:363–377.

Rhoades, C. C., Eckert, G. E., and Coleman, D. C. 2000. Soil carbon differences among forest, agriculture, and secondary vegetation in lower montane Ecuador. Ecological Applications 10:497–505.

Rice, A. Y., Pyle, E. H., Saleska, S. R., Hutyra, L., Palace, M., Keller, M., de Camargo, P. B., Portilho, K., Marques, D. F., and Wofsy, S. C. 2004. Carbon balance and vegetation dynamics in an old-growth Amazonian forest. Ecological Applications 14:S55–S71.

Rudel, T. K., Bates, D., and Machinguiashi, R. 2002. A Tropical forest transition? Agricultural change, out-migration, and secondary forests in the Ecuadorian Amazon. Annals of the Association of American Geographers 92:87–102.

Ruiz, J., Fandiño, M. C., and Chazdon, R. L. 2005. Vegetation structure, composition, and species richness across a 56-year chronosequence of dry tropical forest on Providencia Island, Colombia. Biotropica 47:520–530.

Russell, A. E., Cambardella, C. A., Ewel, J. J., and Parkin, T. B. 2004. Species, rotation, and life-form diversity effects on soil carbon in experimental tropical ecosystems. Ecological Applications 14:47–60.

Saldarriaga, J. G., West, D. C., Tharp, M. L., and Uhl, C. 1988. Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. Journal of Ecology 76:938–958.

Salimon, C. I., Davidson, E. A., Victoria, R. L., and Mello, A. W. F. 2004. CO_2 flux from soil in pastures and forests in southwestern Amazonia. Global Change Biology 10:833–843.

Sánchez-de León, Y., and Zou, X. 2004. Plant influences on native and exotic earthworms during secondary succession in old tropical pastures. Pedobiologia 48:215–226.

Sanger, L. J., Anderson, J. M., Little, D., and Bolger, T. 1997. Phenolic and carbohydrate signatures of organic matter in soils developed under grass and forest plantations following changes in land use. European J of Soil Science 48:311–317.

Saynes, V., Hidalgo, C., Etchevers, J. D., and Campo, J. E. 2005. Soil C and N dynamics in primary and secondary seasonally dry tropical forests in Mexico. Applied Soil Ecology 29:282–289.

Schlesinger, W. H. 1977. Carbon balance in terrestrial detritus. Annual Review of Ecology and Systematics 8:51–81.

Schroth, G., D'Angelo, S. A., Teixeira, W. G., Haag, D., and Lieberei, R. 2002. Conversion of secondary forest into agroforestry and monoculture plantations in Amazonia: consequences for biomass, litter and soil carbon stocks after 7 years. Forest Ecology and Management 163.

Schwendenmann, L., and Pendall, E. 2006. Effects of forest conversion into grassland on soil aggregate structure and carbon storage in Panama: evidence from soil carbon fractionation and stable isotopes. Plant and Soil 288:217–232.

Scow, K. M. 1997. Soil Microbial Communities and Carbon Flow in Agroecosystems. Ecology in Agriculture. Sab Diego, CA: Academic Press.

Silver, W. L., Scatena, F. N., Johnson, A. H., Siccama, T. G., and Watt, F. 1996. At what temporal scales does disturbance affect belowground nutrient pools? Biotropica 28:441–457.

Silver, W. L., Ostertag, R., and Lugo, A. E. 2000a. The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. Restoration Ecology 8:1–14.

Silver, W. L., Neff, J., McGroddy, M., Veldkamp, E., and Keller, M. 2000b. Patterns in soil chemical properties and root biomass along a soil texture gradient in a lowland Amazonian tropical forest. Ecosystems 3:193–201.

Silver, W. L., Kueppers, L. M., Lugo, A. E., Ostertag, R., and Matzek, V. 2004. Carbon sequestration and plant community dynamics following reforestation of tropical pasture. Ecological Applications 14:1115–1127.

Smith, K., Gholz, H. L., and de Assis Oliveira, F. 1998. Litterfall and nitrogen-use efficiency of plantations and primary forest in the eastern Brazilian Amazon. Forest Ecology and Management 109:209–220.

Snedaker, S. C. 1970. Ecological studies on tropical moist forest succession in eastern lowland Guatemala. Ph.D. Thesis. University of Florida, Gainesville.

Soares-Filho, B., Alencar, A., Nepstad, D., Cerqueia, G., Diaz, M. del C. V., Rivero, S., Solórzano, L., and Voll, E. 2004. Simulating the response of land-cover changes to road paving and governance along a major Amazon highway: the Santarém-Cuiabá corridor. Global Change Biology 10:745–764.

Sollins, P., Homann, P., and Caldwell, B. A. 1996. Stabilization and destabilization of soil organic matter: mechanisms and controls. Geoderma 74:65–105.

Sommer, R., Denich, M., and Vlek, P. L. G. 2000. Carbon storage and root penetration in deep soils under small-farmer land-use systems in the Eastern Amazon region, Brazil. Plant and soil 219:231–241.

Spiel, H. 1996. The importance of unpredictable and short-term environmental extremes for biodiversity of Oribatid mites. Biodiversity Letters 3:26–34.

Stern, M., Quesada, M., and Stoner, K. E. 2002. Changes in composition and structure of a tropical dry forest following intermittent cattle grazing. Revista de Biología Tropical 50:1021–1034.

Stevenson, F. J. 1982. Organic matter transformations, distribution, and function in soil. Pages 1–25 in Humus Chemistry: Genesis, Composition, Reactions. Toronto: John Wiley and Sons.

Steward, C. 2007. From colonization to "environmental soy": a case study of environmental and socio-economic valuation in the Amazon soy frontier. Agriculture and Human Values 24:107–122.

Swanston, C. W., Caldwell, B. A., Homann, P. S., Ganio, L., and Sollins, P. 2002. Carbon dynamics during a long-term incubation of separate and recombined density fractions from seven forest soils. Soil Biology and Biochemistry 34:1121–1130.

Swanston, C. W., Torn, M. S., Hanson, P. J., Southon, J. R., Garten, C. T., Hanlon, E. M., and Ganio, L. 2005. Initial characterization of processes of soil carbon stabilization using forest stand-level radiocarbon enrichment. Geoderma 128:63–79.

Szott, L. T., Palm, C. A., and Davey, C. B. 1994. Biomass and litter accumulation under managed and natural tropical fallows. Forest Ecology and Management 67:177–190.

Templer, P. H., Groffman, P., Flecker, A., and Power, A. 2005. Land use change and soil nutrient transformations in the Los Haitises region of the Dominican Republic. Soil Biology and Biochemistry 37:215–225.

Tergas, L. E., and Popenoe, H. C. 1971. Young secondary vegetation and soil interactions in Izabal, Guatemala. Plant and Soil 34:675–690.

Thomlinson, J. R., Serrano, M. I, López, T.del M., Aide, T. M., and Zimmerman, J. K. 1996. Land-use dynamics in a post-agricultural Puerto Rican landscape (1936–1988). Biotropica 28:525–536.

Thomlinson, J. R., and Rivera, L. Y. 2000. Suburban grown in Luquillo, Puerto Rico: some consequences of development on natural and semi-natural systems. Landscape and Urban Planning 40:15–23.

Tiessen, H., Cuevas, E., and Chacon, P. 1994. The role of soil organic matter in sustaining soil fertility. Nature 371:783–785.

Torn, M. S., Trumbore, S. E., Chadwick, O. A., Vitousek, P. M., and Hendricks, D. M. 1997. Mineral control of soil organic carbon storage and turnover. Nature 389:170–173.

Trumbore, S. E. 1993. Comparison of carbon dynamics in tropical and temperate soils using radiocarbon measurements. Global Biogeochemical Cycles 7:275–290.

Trumbore, S. E., Davidson, E. A., de Camargo, P. B., Nepstad, D. C., and Martinelli, L. A. 1995. Belowground cycling of carbon in forests and pastures of Eastern Amazonia. Global Biogeochemical Cycles 9:515–528.

Trumbore, S. E., and Zheng, S. 1996. Comparison of fractionation methods for soil organic matter ^{14}C analysis. Radiocarbon 38:219–229.

Trumbore, S. 2000. Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. Ecological Applications 10:399–411.

Uhl, C., Clark, K., Clark, H., and Murphy, P. 1981. Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon basin. Journal of Ecology 69:631–649.

Uhl, C., Jordan, C., Clark, K., Clark, H., and Herrera, R. 1982. Ecosystem recovery in Amazon caatinga forest after cutting, cutting and burning and bulldozer treatments. Oikos 38: 313–320.

Uhl, C. 1987. Factors controlling succession following slash-and-burn agriculture in Amazonia. Journal of Ecology 75:377–407.

Uhl, C., Buschbacher, R., and Serrão, E. A. S. 1988. Abandoned pastures in Eastern Amazonia. I. Patterns of plant succession. Journal of Ecology 76:663–681.

Veddeler, D., Schulze, C. H., Steffan-Dewenter, I., Buchori, D., and Tscharntke, T. 2005. The contribution of tropical secondary forest fragments to the conservation of fruit-feeding butterflies: effects of isolation and age. Biodiversity and Conservation 14:3577–3592.

Veldkamp, E. 1994. Organic carbon turnover in three tropical soils under pasture after deforestation. Soil Science Society of America Journal 58:175–180.

Vitorello, V. A., Cerri, C. C., Andreaux, F., Feller, C., and Victoria, R. L. 1989. Organic matter and natural carbon-13 distribution in forested and cultivated Oxisols. Soil Science Society of America Journal 53:773–778.

Walker, R. 2003. Mapping process to pattern in the landscape change of the Amazonian frontier. Annals of the Association of American Geographers 93:376–398.

Walker, S. M., and Desanker, P. V. 2004. The impact of land use on soil carbon in Miombo woodlands of Malawi. Forest Ecology and Management 203:345–360.

Walkley, A., and Black, A. 1934. An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. Soil Science Society of America Journal 37:29–38.

Watson, R. T., Noble, I. R., Bolin, B., Ravindranath, N. H., Verando, D. J., and Dokken, D. J, Eds. 2000. Land Use, Land-Use Change, and Forestry. Special Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press.

Weaver, P. L., Birdsey, R. A. and Lugo, A. E. 1987. Soil organic matter in secondary forests of Puerto Rico. Biotropica 19:17–23.

Weaver, P. L., and Birdsey, R. A. 1990. Growth of secondary forest in Puerto Rico between 1980 and 1985. Turrialba 40:12–22.

Weaver, P. L. 1995. Secondary forest management. In Management and Rehabilitation of Degraded Lands and Secondary Forests in Amazonia. Proc. International Symposium/Workshop, ed. J. A. Parrotta and M. Kanashiro, pp. 117–128. Santarém, Pará, Brazil.

Werner, P. 1984. Changes in soil properties during tropical wet forest succession in Costa Rica. Biotropica 16:43–50.

Williams-Linera, G. 1983. Biomass and nutrient content in two successional stages of tropical wet forest in Uxpanapa, Mexico. Biotropica 15:275–284.

Wright, J. A., DiNicola, A., and Gaitan, E. 2000. Latin American forest plantations: opportunities for carbon sequestration, economic development, and financial returns. Journal of Forestry 98:20–23.

Yan, E.-R., Wang, X.-H., and Huang, J.-J. 2006. Shifts in plant nutrient use strategies under secondary forest succession. Plant and Soil 289:187–197.

Zarin, D. J., Davidson, E. A., Brondizio, E., Vieira, I. C. G, Sá, T., Feldpausch, T., Schuur, E. A. G, Mesquita, R., Moran, E., Delamonica, P., Ducey, M. J., Hurtt, G. C., Salimon, C., and Denich, M. 2005. Legacy of fire slows carbon accumulation in Amazonian forest regrowth. Frontiers in Ecology and the Environment:365–369.

Zimmerman, J. K., Aide, T. M., Rosario, M., Serrano, M., and Herrera, L. 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. Forest Ecology and Management 77:65–76.

Zou, X., Zucca, C. P., Waide, R. B., and McDoweel, W. H. 1995. Long-term influences of deforestation on tree species composition and litter dynamics of a tropical rain forest in Puerto Rico. Forest Ecology and Management 78:147–157.