The Potential for Carbon Sequestration Through Reforestation of Abandoned Tropical Agricultural and Pasture Lands

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Abstract

Approximately half of the tropical biome is in some stage of recovery from past human disturbance, most of which is in secondary forests growing on abandoned agricultural lands and pastures. Reforestation of these abandoned lands, both natural and managed, has been proposed as a means to help offset increasing carbon emissions to the atmosphere. In this paper we discuss the potential of these forests to serve as sinks for atmospheric carbon dioxide in aboveground biomass and soils. A review of literature data shows that aboveground biomass increases at a rate of 6.2 Mg ha^{-1} yr^{-1} during the first 20 years of succession, and at a rate of 2.9 Mg ha^{-1} yr^{-1} over the first 80 years of regrowth. During the first 20 years of regrowth, forests in wet life zones have the fastest rate of aboveground carbon accumulation with reforestation, followed by dry and moist forests. Soil carbon accumulated at a rate of 0.41 Mg ha^{-1} yr^{-1} over a 100-year period, and at faster rates during the first 20 years (1.30 Mg carbon ha^{-1} yr^{-1}). Past land use affects the rate of both above- and belowground carbon sequestration. Forests growing on abandoned agricultural land accumulate biomass faster than other past land uses, while soil carbon accumulates faster on sites that were cleared but not developed, and on pasture sites. Our results indicate that tropical reforestation has the potential to serve as a carbon offset mechanism both above- and belowground for at least 40 to 80 years, and possibly much longer. More research is needed to determine the potential for longer-term carbon sequestration for mitigation of atmospheric CO_2 emissions.

Key words: soil carbon, plant carbon, land use, tropical forest, carbon accumulation, global change, carbon offset.

Introduction

Fifty-two percent of the world's forests are concentrated in the tropics, which have the highest rates of deforestation and land conversion globally (Brown et al. 1996*a*). Tropical deforestation and land use change have a significant impact on the global carbon cycle through increased rates of C emissions to the atmosphere and the loss of above- and belowground C accumulation and storage capacity. Current estimates suggest that approximately 1.6 (± 0.5) Pg (petagram = 10^{15} g) of C are lost annually from the conversion of tropical forests (Brown et al. 1996*b*). The tropical forest biome is generally considered a net source of CO_2 to the atmosphere as compared to mid and high latitude forests (Houghton et al. 1993), which act as sinks for atmospheric CO_2 (but see Lugo 1992*a*; Lugo & Brown 1992).

At the turn of the century, Clarke (1908) suggested that photosynthetic activity by plants had the potential to mitigate anthropogenically produced atmospheric CO_2 over large areas. However, it was not until the early 1990s that systematic efforts were made to identify natural terrestrial sinks of atmospheric C and provide information about the management of biota to sequester C (Wisniewski & Lugo 1992). Today, there is considerable interest in identifying C sequestration mechanisms in the environment (Bouman et al. 1999), international protocols for tracking C sequestration are being developed (Brown et al. 1996*b*), and proposals for managing forest lands for C storage are becoming increasingly common (Brown et al. 1996*a*,*b*; Fearnside & Guimaraes 1996). Carbon sequestration is now a recognized forest management strategy with enormous economic implications, due primarily to the advent of "carbon credits." Carbon credits are awarded to entities ranging from companies to countries, and allow C emissions above

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levels negotiated in international treaties in exchange for a proportional C sink established on the landscape.

One of the proposed strategies to help mitigate atmospheric C emissions is to reforest and restore tropical forests from abandoned and degraded agricultural and pasture lands (Houghton et al. 1993). Restoration and reforestation have the potential to contribute to C storage directly through biomass and soil C accumulation (Richter et al. 1999), and indirectly by providing an alternative to fossil fuels for energy generation (Fearnside 1999). Increased C storage can be achieved by augmenting the land area covered in forest and/or by increasing the C density of forests (Brown et al. 1996*a*). This is likely to be a finite process, however; biomass may eventually reach a maximum sequestration potential and no longer reduce the amount of CO_2 in the atmosphere. The time period this requires is not well known, but it has been speculated that such a limit is reached in the first 50–100 years following forest establishment. Alternatively, the use of biomass products as renewable fuels can provide a longer-term mechanism for offsetting increased atmospheric CO_2 (Brown et al. 1996*a*; Fearnside 1999). This approach requires careful accounting of the loss of C sequestration potential associated with harvesting, and of the amount of fossil fuel conserved by substituting a biomass product for a fossil fuel source. Through this type of fuel substitution, forest management is encouraged, and the use and productivity of reforested areas can be extended.

Forests where trees have rapid growth rates, such as many tropical plantations and natural successions, are excellent options for mitigating CO_2 emissions through C sequestration (Montagnini & Porras 1998). Winjum et al. (1992) estimated that 52–104 Pg of C could be sequestered over 50 years through reforestation and afforestation globally, with approximately 70% occurring in tropical latitudes. Research on tropical forest secondary succession suggests that significant amounts of C can accumulate in plants and soils over relatively short ($\sim$20 yr) time periods (Brown & Lugo 1992). Few studies have examined longer-term rates of C accrual, although aboveground C pools frequently exceed 100 Mg/ha in humid secondary forests after 50 years (Lugo & Brown 1992). The relative distribution of C accumulated in soils and plants is not well documented, but C is generally thought to accumulate more rapidly aboveground than belowground, and some belowground C pools are likely to have slower turnover times and thus have the potential for longer-term C storage.

Forest composition and structure, land-use history, and climate are all likely to affect the rate and character of C sequestration. For example, tropical plantation species are often chosen for their ability to allocate a high proportion of C to stem wood, while evidence suggests that natural secondary forests may allocate proportionally more C to roots (Cuevas et al. 1991; Lugo 1992*b*). Mature, natural forests in moist life zones tend to have greater aboveground C stores than wet or dry forests (Brown & Lugo 1982), although seasonally dry forests tend to allocate considerable C to belowground biomass (Brown & Lugo 1982; Murphy & Lugo 1986*a,b*; Nepstad et al. 1994).

The large area of secondary forests in the tropics and the commercialization of C sequestration raise numerous questions of ecological interest. What ecosystems are the best C sinks? What is the relative importance of above- and belowground C sinks in forests? How fast can C be sequestered in forests and what factors affect this rate? Can rates of C sequestration be accelerated? In this paper, we briefly review the literature on rates of C accumulation with reforestation in the tropics, and use literature data to explore the effects of reforestation on above- and belowground C pools. We focus on secondary forests, which colonize the majority of abandoned lands in the tropics (Lugo & Brown 1992). Patterns of C accumulation during secondary succession are likely to offer many valuable clues for successful forest restoration. We explore general patterns in C accumulation and storage with reforestation in relation to stand age, climate, and land use history, and examine the potential for reforestation to provide a C offset alternative for tropical countries.

Aboveground Biomass

Tropical forests are well known for high rates of net primary production and store approximately 216 Pg C in the aboveground biomass (Brown et al. 1993; Dixon et al. 1994). Moist tropical forests tend to have more aboveground biomass than wet or dry tropical forests (Brown & Lugo 1982). A significant proportion of the tropical forest biome is in some state of recovery from past human disturbance. Lugo and Brown (1993) estimated that there were approximately 490×10^6 ha of mature tropical forest in the 1980s, and 540×10^6 ha of tropical forests that had been logged, cleared, fallowed, or were in plantations. Recovering forests are likely to accumulate C at a rapid rate and serve as net sinks for CO_2. The accumulation of aboveground biomass performs many important ecosystem functions in addition to storing C, including reducing erosion and nutrient leaching, ameliorating microclimatic conditions, and providing shelter and structural complexity for wildlife. Thus, many studies on secondary succession have focused on documenting pools of aboveground biomass and rates of biomass accumulation with time.

Tropical secondary forests have been reported to accumulate up to 5 Mg C ha^{-1} yr^{-1} during the first 10 to 15 years of regrowth (Brown & Lugo 1990*b*), and on average have been estimated to sequester 2–3.5 Mg C ha^{-1}

yr^{-1}. Although secondary forests may not produce the same high volumes of timber per unit area and time as plantations, they are still suitable ecosystems for C sequestration. In fact, secondary forests and forest fallows are the most important form of C recovery in tropics due to the extensive area involved (Lugo & Brown 1992). Because of the low inputs and capital investments needed for biomass establishment, secondary forests may also be useful ecosystems for fuel substitution mitigation.

The patterns of biomass accumulation with time differ between plantations and secondary forests. Plantation species are often selected for rapid aboveground growth and, thus, usually gain aboveground biomass faster than secondary forests under the same edaphic and climatic conditions (Lugo 1992*b*). Rates of biomass gain in plantations are subject to the same constraints as secondary forests, with a few important exceptions. Species for plantations can be chosen for rapid establishment and amelioration of soils and microclimate conditions (Lugo et al. 1993; Brown & Lugo 1994). Natural secondary forests may require longer time periods to "sort out" appropriate species for successful establishment, particularly when propagules are limiting. Plantations are often less diverse than natural secondary forests, although diversity in the understory can be close to that of natural systems (Lugo 1992*b*). Lower diversity may lead to greater susceptibility to insect and pathogen attack. Lower diversity may also lead to increased susceptibility to catastrophic disturbance events, such as hurricanes or fires, although the presence of individual species that are specifically adapted to particular disturbances may be more important than diversity per se (Silver et al. 1996). These factors can all feedback on rates and patterns of C sequestration. Rates of aboveground C accumulation in plantations range from 0.8 to 15 Mg C ha^{-1} yr^{-1}, during the first 26 years following establishment (Lugo et al. 1988). A review of the literature for seven common tropical plantation species showed that most species generally grew best in moist climates as opposed to wet or dry life zones similar to natural forests, although each species had a particular optimum climate for aboveground growth (Lugo et al. 1988).

Soil Carbon

Tropical forests store approximately 206 Pg C in the soil (Eswaran et al. 1993), about twice as much as mid-latitude forests, but less than half that of boreal forests (Brown et al. 1993; Dixon et al. 1994). Wet and moist tropical forests tend to have greater soil C pools per unit area than tropical dry forests due to higher rates of NPP (Brown & Lugo 1982), and also have faster rates of C turnover in the soil (Raich & Schlesinger 1992). Soil C pools play an important role in ecosystem biogeochemical cycling and the maintenance of net primary productivity. Soil organic matter, of which about half is soil C, is both a source of nutrients and water to plants and microbes, and a site for nutrient and water retention. Much of the cation exchange capacity in highly weathered tropical soils occurs on organic colloids (Tiessen et al. 1994).

Deforestation can result in an initial loss of C from soils because of increased decomposition rates, erosion, reduced inputs, or inputs of different quality (herbaceous vs. woody litter) (Lugo & Brown 1993). Carbon dynamics following deforestation depend upon the type and intensity of land use practices and climate. For example, burning is likely to decrease soil C stocks (Ewel et al. 1981), and may require longer time periods for recovery. Not all land uses result in a loss of soil C. In tropical pastures, soil C pools have been shown to both increase (Chone et al. 1991) and decrease (Detwiler 1986; Veldkamp 1994) over time. The gain or loss of soil C with reforestation is likely to depend strongly on the intensity of past land use practices. Intensive pasture management in Brazil resulted in lower soil C pools eight years following reforestation than sites that were less intensively used (Buschbacher et al. 1988). The effects of climate on soil C accumulation with reforestation are not well known. In mature tropical forests, soil C pools tend to decrease exponentially as the ratio of temperature to precipitation increases, corresponding to a gradient from wet to dry forests (Brown & Lugo 1982).

Patterns in Carbon Accumulation with Reforestation

We used data from the literature to examine patterns in aboveground biomass and soil C following reforestation in the tropics. For aboveground biomass we limited our analysis to secondary succession (Appendix 1). Plantations have been reviewed elsewhere (Lugo et al. 1988; Lugo & Brown 1992). All sites were completely cleared and the majority of them were also burned prior to forest regrowth. As is common with literature studies, our analyses are limited by some methodological issues. There are considerably more data points for the first few years of regrowth than for later stages of succession. In addition, the choice of biomass equation used in individual studies is likely to strongly influence values (Alves et al. 1997). We examine patterns with past land use (agriculture, pasture, or cleared and abandoned), using the most recent land use specified by the authors. We also examined patterns across general life zone categories. Life zone categorizations were determined by the authors, or were estimated from total annual rainfall reported in the studies according to the following classifications: dry ($<$1,000 mm/yr), moist (1,000–2,500 mm/yr), and wet ($>$2,500 mm/yr). Data are given in Appendix 1.

To examine patterns in soil C pools with reforestation, we compiled data from the literature that reported forest age together with soil C content or soil C concentrations and bulk density values (Appendix 2). We used data from both natural secondary succession and plantations, because these data have not been thoroughly reviewed elsewhere. We examine patterns with regard to the same land use and life zone categories as for aboveground biomass. When organic matter was reported we used a conversion factor of 0.5 to estimate soil C pools. Studies reported a variety of depths ranging from 7 to 50 cm, but were conducted predominantly in the top 25 cm. In an effort to roughly standardize depths across studies, we used a regression technique to determine the relationship of soil C pools with depth (Silver et al. 2000). For the literature data set, soil C in wet life zones decreased with depth according to the linear equation $y = 1.13\times + 0.51$ ($r^2 = 0.82$, $p < 0.01$, $n = 39$) using log-transformed data for depth and C content. The moist forest data set was smaller and did not show a significant trend with depth. For these data we used an equation developed by Silver et al. (2000) for moist forests in Amazonia ($y = 0.99\times + 8.50$, $r^2 = 0.87$, $p < 0.01$, $n = 30$). We used this equation for dry forests as well because there were no equivalent equations available for dry forest life zones. Although this approach is less than ideal, it provides a preliminary frame of reference to allow comparisons across studies. Lugo and Brown (1993) compared soil C across studies by using the ratio of soil in the disturbed site to a mature site sampled to the same depth in the same studies. Unfortunately, many studies do not report soil C for mature forest sites. Furthermore, deforested sites may be chosen for particular soil qualities such as high soil organic matter, better drainage, or flat topography that may differ from nearby forests. Soil data were used for forests with greater than 3 years since abandonment or plantation establishment.

Data were analyzed using linear and log-linear regressions in Systat 7.0 (Wilkinson 1990). We examine data for patterns in soil C pools with forest age (years), life zone (wet, moist, dry), and previous land use prior to reforestation or abandonment (cleared and abandoned, pasture, agricultural crops). We used *t*-tests to compare cover types (soil only, plantation or natural succession), and ANCOVA to examine the rate of change in soil C accumulation over time in different life zones and with previous land use.

Rates of Aboveground Biomass Accumulation

Aboveground biomass increased significantly with time following reforestation (Table 1), similar to results reported previously (Brown & Lugo 1990*a*). The overall rate of aboveground biomass accumulation was 2.36 Mg ha^{-1} yr^{-1}. Most studies have examined only the first 20 years of forest regrowth; here the rate of aboveground biomass accumulation was significantly faster during the first 20 years of regrowth (6.17 Mg ha^{-1} yr^{-1}) than over the subsequent 60 year period ($p < 0.01$).

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

Parameter	*Equation*	r^2	p	n
	All Ages			
All data	ln (BIOMASS) = ln*(0.76*AGE) + 2.08	0.66	<0.01	143
Life zone				
Moist forests	ln (BIOMASS) = ln*(0.70*AGE) + 2.25	0.72	<0.01	90
Wet forests	ln (BIOMASS) = ln*(0.96*AGE) + 1.56	0.65	<0.01	44
Dry forests	n.s.			9
Past land use				
Agriculture	ln (BIOMASS) = ln*(0.77*AGE) + 2.17	0.78	<0.01	100
Pasture	BIOMASS = ln*(21.14*AGE) + 1.22	0.33	<0.01	22
Cleared	BIOMASS = ln*(11.46*AGE) − 3.03	0.86	<0.01	6
	Forests 0 to 20 Years Old			
All data	ln (BIOMASS) = ln*(0.84*AGE) + 1.99	0.58	<0.01	116
Life zone				
Moist forests	ln (BIOMASS) = ln*(0.73*AGE) + 2.12	0.60	<0.01	74
Wet forests	ln (BIOMASS) = ln*(1.11*AGE) + 1.39	0.61	<0.01	32
Dry forests	ln (BIOMASS) = (0.16*AGE) + 2.49	0.81	<0.01	8
Past land use				
Agriculture	ln (BIOMASS) = ln*(0.81*AGE) + 2.12	0.70	<0.01	81
Pasture	ln (BIOMASS) = ln*(0.72*AGE) + 1.92	0.18	= 0.08	18
Cleared	n.s.			5

Note. n.s., not significant.

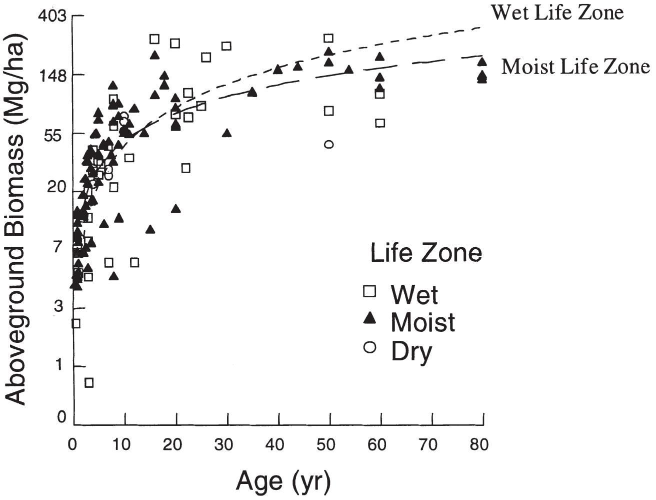

Figure 1. Aboveground biomass (Mg/ha) with age (years) and life zone in reforested tropical ecosystems. Data are listed in Appendix 1. Life zone categorizations were determined by the authors, or were estimated from total annual rainfall reported in the studies according to the following classifications: dry (<1,000 mm/yr), moist (1,000–2,500 mm/yr), and wet (>2,500 mm/yr). Data for dry forests did not vary significantly with age. See Table 1 for best fit regression equations. Note that the y-axis is a log scale.

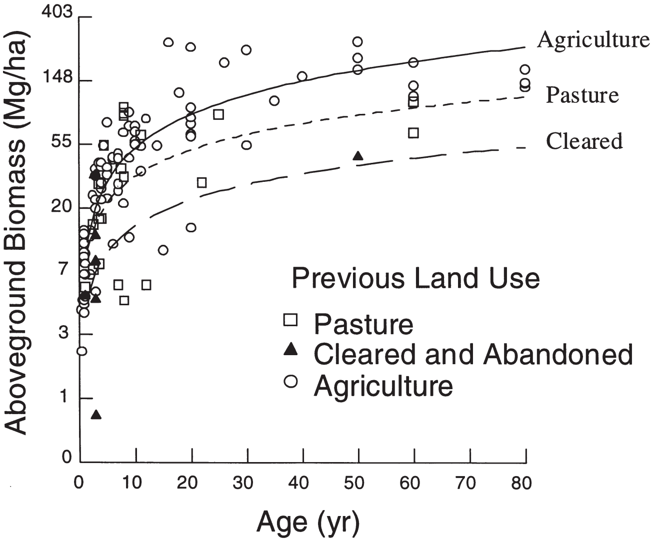

Figure 2. Aboveground biomass (Mg/ha) with age (yr) and previous land use in reforested tropical ecosystems. Data are listed in Appendix 1. See Table 1 for best fit regression equations. Note that the y-axis is a log scale.

There was no effect of life zone during the first 20 years of regrowth, but wet forests accumulated C faster than moist forests during the 20 to 80 year period ($p = 0.07$). Overall (80 yr), wet forests accumulated biomass at a rate 3.24 Mg ha^{-1} yr^{-1} ($n = 44$) and moist forests at a rate of 2.17 Mg ha^{-1} yr^{-1} ($n = 91$), while dry forests showed no significant pattern with time (Table 1; Fig. 1).

Land use also had a significant effect on aboveground biomass gain with reforestation ($p = 0.07$). Forests regrowing on old agricultural fields accumulated biomass at slightly faster rates than forests grown on abandoned pastures (Fig. 2). Sites that were cleared but not cultivated showed the slowest rate of aboveground regrowth, but these sites also had the smallest sample size. It is possible that crops or pasture were not successful at these sites due to nutrient, water, pest, or physical factors that could also inhibit forest regeneration. During the first 20 years of regrowth, there was a strong significant increase in aboveground biomass following agricultural use, but not with other land uses (Table 1). The rate of aboveground regrowth in abandoned agricultural fields was 6.04 Mg ha^{-1} yr^{-1} during the first 20 years.

Although we were unable to address the effects of species composition, species affect C sequestration due to their allocation patterns and growth form. For example, grasses, ferns, and other herbaceous vegetation that tend to dominate early on in succession have much less aboveground C accumulation than woody vegetation (Aide et al. 1995). Some restored areas may undergo "arrested" succession where tree regeneration is impeded by grasses or ferns, and thus aboveground biomass accumulation may be much lower than what would be predicted from Figure 2.

Soil Carbon Accumulation with Reforestation

There was a statistically significant relationship between soil C content and forest age during the first 100 years following establishment, although the predictive power of the relationship was low (Table 2). During the first 20 years of forest establishment, soil C pools averaged 60 ± 4 Mg C/ha ($n = 33$); this increased significantly to 74 ± 6 Mg C/ha ($n = 24$) during the subsequent 20–100 years ($p < 0.01$). Soil C pools in mature forests were 72 ± 7 Mg C/ha ($n = 12$). Soil C accumulated at a rate of 1.30 Mg ha^{-1} yr^{-1} during the first 20 years and at a rate of 0.20 Mg ha^{-1} yr^{-1} for the subsequent 80 year period.

Overall, soil C accumulated at a rate of 0.41 Mg ha^{-1} yr^{-1} over a 100 year period following reforestation. There were no strong patterns in the rate of soil C accumulation with life zone, in contrast to data reported by Weaver et al. (1987). Moist forests accumulated soil C at a rate of 0.51 Mg ha^{-1} yr^{-1}, which was a slightly slower rate ($p < 0.10$) than dry forests (1.02 Mg ha^{-1} yr^{-1}). Wet forests did not show a significant increase in soil C pools over time. Dry forest sites followed a strongly significant linear increase in soil C with time (Table 2), although it is important to note the relatively small sample size for this life zone. The rapid rate of soil C

Table 2. Regression equations for soil carbon (Mg/ha) with time following tropical reforestation. See Appendix 2 for data.

Parameter	*Equation*	r^2	p	n
	All Ages			
All data	ln(SOIL C) = 0.16*ln(AGE) + 3.65	0.11	<0.05	57
Life zone				
Moist forests	ln(SOIL C) = 0.25*ln(AGE) + 3.31	0.23	<0.05	22
Wet forests	n.s.			23
Dry forests	ln(SOIL C) = 0.384*ln(AGE) + 2.98	0.99	<0.01	5
Past land use				
Agriculture	n.s.			18
Pasture	ln(SOIL C) = 0.177*ln(AGE) + 3.47	0.14	= 0.09	21
Cleared	ln(SOIL C) = 0.277*ln(AGE) + 3.59	0.27	= 0.08	12
	Forests 0 to 20 Years Old			
All data	ln (SOIL C) = 0.03*ln(AGE) + 3.76	0.12	= 0.05	33
Life zone				
Moist forests	n.s.			10
Wet forests	n.s.			22
Dry forests	n.s.			2
Past land use				
Agriculture	n.s.			12
Pasture	ln (SOIL C) = 0.04*ln(AGE) + 0.36	0.24	= 0.08	14
Cleared	n.s.			7

Note. n.s., not significant.

accumulation in dry forests contradicts estimates published previously (Lugo & Brown 1993). The differences noted in our analysis from past studies may be related to land use practices in dry tropical regions. When a choice is possible, the best, most fertile soils are generally chosen for agricultural development or pasture establishment. Our data show that dry forests had high soil C to begin with, differing from data reported for mature tropical forests (Brown & Lugo 1982). This may be due to site selection for soils with higher organic matter content and thus better fertility, structure, and water holding capacity.

Past land use had an impact on the rate of soil C accumulated with reforestation ($p < 0.01$), although patterns are much less clear than for aboveground biomass (Table 2). Sites that were deforested but not managed prior to forest re-establishment tended to accumulate soil C at a faster rate (1.17 Mg C ha^{-1} yr^{-1}; $n = 12$), than pasture sites (0.49 Mg ha^{-1} yr^{-1}; $n = 21$), or agricultural sites (0.25 Mg ha^{-1} yr^{-1}; $n = 12$). This effect was not apparent during the first 20 years of forest recovery, but was strongly significant ($p < 0.01$) during the subsequent 80 years. The rate of change in soil C accumulation differed significantly over time (Fig. 3; $p < 0.01$), with fastest rates early in forest development for all three previous land use types. There was no distinguishable effect of cover type (plantation versus natural secondary succession) on the rates of soil C accumulation following reforestation, although plantations had significantly ($p < 0.01$) more soil C (90 ± 9 Mg C/ha, $n = 10$) than secondary forests (61 ± 3 Mg C/ha, $n =$ 47). Lugo and Brown (1993) found low soil C in tree plantations and suggested that this may be due to the fact that plantations are often established on degraded lands. They also found that soil C accumulation was highly species dependent due to differences in litter production, litter quality, microclimate changes, and changes in edaphic conditions.

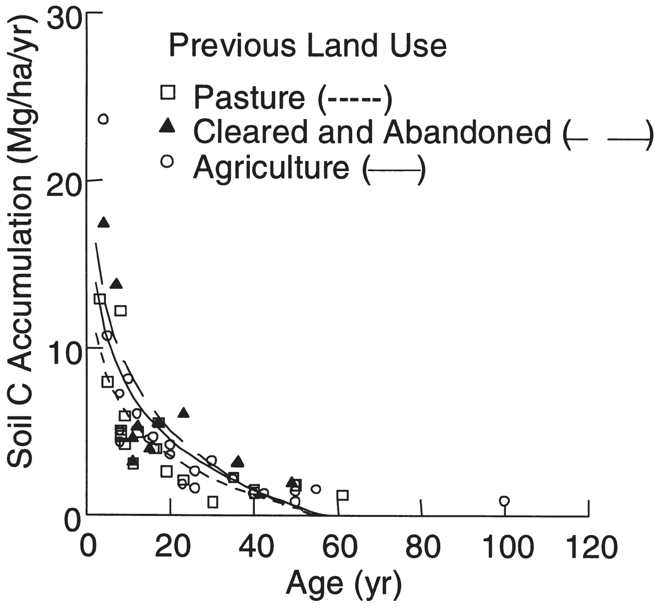

Figure 3. The rate of change in soil C accumulation with age over time and by previous land use. Data are given in Appendix 2.

Bashkin and Binkley (1998) found that the establishment of *Eucalyptus* plantations on sugar cane fields led to a gain of C in surface soils (0–10 cm depth), but a corresponding loss of C from subsoils (10–40 cm depth), leading to a net deficit of soil C 11 years after forest establishment. In this analysis we have focused only on surface soils. The loss of C from subsurface horizons raises an important issue for C sequestration projects. The depth to which soils are to be monitored to account for soil C gains and losses will be an important consideration in C mitigation programs.

Reforestation as a Carbon Offset Approach

Brown (1998) suggested three strategies for accomplishing C sequestration objectives through forest management: conserving forests, building C storage in soils and biomass through reforestation and afforestation, and substituting biomass for fossil fuels. Our review of the literature on the rate of C accumulation in tropical secondary forests reveals five insights to this process.

First, we documented the importance of the previous land use on the rate of C sequestration in vegetation and soils. When the previous land use results in low degradation or high relative fertility, such as some types of fertilized agriculture, biomass accumulation through succession is faster than when the previous land use degrades the site for aboveground regrowth, as was the case for pastures in our analysis. Intensive pasture management can result in low soil fertility and soil compaction reducing soil aeration and biological activity (Lavelle & Pashanasi 1989). In contrast, agricultural fields are often fertilized, either with chemical fertilizers or organic mulches that can improve nutrient availability and soil structure (Sanchez 1976). Soils accumulated more C when sites were not managed or were in pasture. Pasture grasses allocate considerable C belowground and thus have the potential to increase soil C pools (Chone et al. 1991). Compaction associated with pasture use may lead to slower rates of decomposition in soils and thus lower rates of soil C loss (Lavelle & Pashanasi 1989; Veldkamp 1994). The reduction in the rate of C accumulation or succession due to site degradation by previous land use has been termed a "time tax," because time or heavy subsidies are needed to overcome the degradation from past land use, similar to a tax on resource utilization (Lugo 1988). Our analysis highlights the importance of considering past land use when evaluating a site's potential for C sequestration.

Second, we observed a different pattern in the rate of aboveground and belowground C accumulation in dry forests than would be expected from data on mature forests in dry life zones. Dry successional forests accumulated soil C at a faster rate than wet or moist forests. This high resiliency might be due to high root biomass in these forests and their ability to resprout following clearcutting (Ewel 1977; Murphy & Lugo 1986*a,b*). This mechanism for fast accumulation of belowground C prevails if root biomass is not harmed by previous land uses. As already mentioned, site selection for agriculture or pasture establishment may also favor high C soils.

Third, we observed a continuous accumulation of aboveground biomass in forests up to 80 years of age (the length of the available data set). The rate of sequestration varied with life zone as previously shown (Brown & Lugo 1990*a*), and slowed over time. Our results showed that soil C accumulated faster for approximately 20 years in the top 25 cm of mineral soil, than later in forest development. While this is likely to be the most active zone for C accumulation over short time periods, the dynamics of deeper soil profiles are important to consider, especially when planning for long term C sequestration. Schlesinger (1990), considering the entire depth profile, suggested that soil organic C accumulation continues for millennia, which means that reforested stands may continue to sequester C for long periods of time and cannot be assumed to reach steady state as they age.

Fourth, short-term measurements of C accumulation resulted in larger C sequestration values than when biomass and soil values are divided by longer time intervals. This is both a methodological and ecological issue. The rate of C accumulation over time decreases in part because there is a limit on the amount of C that can accumulate per unit area; this is particularly true for aboveground biomass. Maximum biomass accumulation is approached as an asymptote. Measurements made over short time intervals are always likely to yield higher values than long time intervals because trees are long-lived organisms, and canopy closure, and thus high occupancy rates, are achieved relatively early in their life cycle. It is also important to note that the precision in estimates of rate processes is likely to decrease as the time interval of the measurement increases.

Fifth, the allocation of biomass above- or belowground is likely to be both species and community specific, and has relevance to the persistence of sequestered C. Carbon stored belowground is often assumed to have a longer residence time than C stored aboveground, although recent analyses have shown that in some ecosystems the majority of soil C may turn over on the scale of tens of years (Trumbore 1993). Grasses and some tree species store more C belowground than aboveground. Other tree species, particularly plantation species, store more C aboveground. Therefore, forest managers can influence the storage of C by selecting species or ecosystem types for their C allocation strategies.

Can restoration and reforestation efforts be justified for C offsets? Our analysis clearly shows that there is great potential for above- and belowground C sequestration with reforestation. However, there are several issues that must still be resolved to assure viable C offset programs. First, the protocol for estimating C pools and fluxes needs to be standardized. Carbon storage estimates currently depend on which pools are measured, the biomass equations developed, and the types of laboratory analyses used (Brown 1998). In addition, more data from older (>50 yr) secondary forests are needed to determine long term trends and realistic project timetables (Finegan 1996). The use of forests as a C offset must take into consideration the impacts of human activities or natural disturbances, both of which can lead to transfers of C from live to dead pools (Pinard & Putz 1996), and losses to the atmosphere. Finally, carbon offset policy will need to address how C sequestration will be altered with global climate change (Brown et al. 1996*a*). Evidence suggests that tropical forests C pools and fluxes are likely to be sensitive to even small changes in temperature and precipitation associated with rising atmospheric CO_2 (Townsend et al. 1992; Silver 1998). Increases in atmospheric CO_2 may lead to greater total net primary productivity, but the limits of this increase for C sequestration have yet to be determined (but see DeLucia et al. 1999). These issues present exciting challenges for researchers in the fields of ecological restoration and forest succession. The reforestation of abandoned agricultural and pasture land offers many ecological and societal benefits, and is also likely to provide an important economic justification to maintain forest cover in many tropical countries.

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Appendix 1. Total aboveground live biomass pools in forests of known age following tropical reforestation. Life zones are wet (W), moist (M), and dry (D) based on authors' descriptions or estimates from total annual rainfall (see Figure 1). Past land uses, when given in the reference, are agriculture (A), pastures (P), or cleared and then abandoned (C).

Age yr	*Life Zone*	*Past Land Use*	*Biomass Mg/ha*	*Reference*
0.3	M	A	4	Szott et al. 1994
0.5	W	A	2	Hughes et al. 1999
0.7	M	A	5	Szott et al. 1994
0.8	M	A	4	Tergas & Popenoe 1971
0.8	M	A	9	Tergas & Popenoe 1971
0.8	M	A	12	Tergas & Popenoe 1971
0.8	M	A	100	Tergas & Popenoe 1971
0.8	M	A	9	Tergas & Popenoe 1971
0.8	M	A	7	Tergas & Popenoe 1971
0.8	M	A	4	Tergas & Popenoe 1971
0.8	M	A	13	Tergas & Popenoe 1971
0.8	M	A	14	Tergas & Popenoe 1971
0.8	M	A	14	Tergas & Popenoe 1971
0.8	W	A	5	Williams-Linera 1983
1	M	A	10	Drew et al. 1978
1	W	C	5	Silver et al. 1996
1	M	A	8	Snedaker 1970
1	M	A	5	Toky & Ramakrishnan 1983
1	W	A	7	Uhl 1987
1	M	A	6	Uhl et al. 1988
1.4	M	A	13	Szott et al. 1994
2	M	A	7	Alves et al. 1997
2	M	A	13	Ewel 1971
2	M		19	Fölster et al. 1976
2	M	A	14	Snedaker 1970
2	W	A	13	Uhl 1987
2.4	M	A	25	Szott et al. 1994
2.5	M	P	16	Uhl et al. 1988
2.5	M	P	8	Uhl et al. 1988
2.8	M	C	33	Maury-Lechon 1982
3	M	A	37	Alves et al. 1997
3	M	A	33	Alves et al. 1997
3	M	A	5	Drew et al. 1978
3	W	C	5	Nykvist 1996
3	M	A	23	Snedaker 1970
3	W	C	9	Uhl et al. 1982
3	W	C	1	Uhl et al. 1982
3	W	C	13	Uhl et al. 1982
3	W	A	20	Uhl 1987
3.5	M	P	17	Uhl et al. 1988
3.5	M	P	29	Uhl et al. 1988
3.5	M	P	8	Uhl et al. 1988
3.6	M	A	41	Szott et al. 1994
4	M	A	38	Ewel 1971
4	M	A	41	Hughes et al. 1999
4	D	A	23	Sabhasri 1978
4	D	A	30	Sabhasri 1978
4	M	A	27	Snedaker 1970
4	W	A	29	Uhl 1987
4	M	P	17	Uhl et al. 1988
4.4	M	A	53	Szott et al. 1994
4.5	M	P	53	Uhl et al. 1988
5	M	A	38	Alves et al. 1997
5	M	A	77	Bartholomew et al. 1953
5	M		68	Fölster et al 1976
5	W		27	Nykvist 1996
5	M	A	37	Snedaker 1970
5	M	A	23	Toky & Ramakrishnan 1983
5	W	A	34	Uhl 1987
5.5	W		32	Lugo 1992*b*
6	M	A	11	Drew et al. 1978
6	M	A	43	Ewel 1971
6	M	A	45	Snedaker 1970
7	W	P	6	Aide et al. 1995
7	D	A	29	Sabhasri 1978
7	D	A	26	Sabhasri 1978
7	M	A	47	Snedaker 1970
7	W	A	43	Williams-Linera 1983
7.5	M	P	37	Uhl et al. 1988
8	M	A	122	Bartholomew et al. 1953
8	W	A	22	Hughes et al. 1999
8	W	P	97	Hughes et al. 1999
8	W		62	Nykvist 1996
8	M	A	66	Snedaker 1970
8	M	P	89	Uhl et al. 1988
8	M	P	86	Uhl et al. 1988
8	M	P	33	Uhl et al. 1988
8	M	P	5	Uhl et al. 1988
9	M	A	90	Alves et al. 1997
9	M	A	13	Drew et al. 1978
9	M	A	44	Saldarriaga et al. 1988
9	M	A	72	Snedaker 1970
10	D	A	66	Sabhasri 1978
10	D	A	73	Sabhasri 1978
10	D	A	56	Sabhasri 1978
10	D	A	57	Sabhasri 1978
10	M	A	54	Snedaker 1970
10	M	A	58	Toky & Ramakrishnan 1983
11	M	P	63	Alves et al. 1997
11	W	A	36	Cuevas et al. 1991
11	M	A	53	Saldarriaga et al. 1988
12	W	P	6	Aide et al. 1995
12	M	A	82	Saldarriaga et al. 1988
14	M	A	53	Saldarriaga et al. 1988
15	M	A	10	Toky and Ramakrishnan 1983
16	M		103	Alves et al. 1997
16	M		203	Fölster et al. 1976
16	W	A	272	Hughes et al. 1999
18	M		143	Alves et al. 1997
18	M	A	123	Greenland & Kowal 1960
20	M	A	60	Drew et al. 1978
20	W	A	76	Hughes et al. 1999
20	W	A	253	Hughes et al. 1999
20	M	A	62	Saldarriaga et al. 1988
20	M	A	98	Saldarriaga et al. 1988
20	M	A	64	Saldarriaga et al. 1988
20	M	A	83	Saldarriaga et al. 1988
20	M	A	15	Toky & Ramakrishnan 1983
22	W	P	30	Aide et al. 1995
22.5	W		72	Lugo 1992*b*
22.5	W		109	Lugo 1992*b*
25	W	P	88	Aide et al. 1995
26	W	A	199	Hughes et al. 1999

Continued

Appendix 1. Continued.

Age yr	*Life Zone*	*Past Land Use*	*Biomass Mg/ha*	*Reference*
30	M	A	54	Saldarriaga et al. 1988
30	W	A	241	Hughes et al. 1999
35	M	A	109	Saldarriaga et al. 1988
35	M	A	108	Saldarriaga et al. 1988
40	M	A	159	Saldarriaga et al. 1988
44	M		165	Jordan & Farnworth 1982
50	M	A	214	Greenland & Kowal 1960
50	W		80	Lugo 1992*b*
50	W	A	274	Hughes et al. 1999
50	D	C	45	Singh 1975
50	M	A	178	Singh & Ramakrishnan 1982
54	M	P	158	Silver et al. 2001
60	W	P	65	Aide et al. 1995
60	W	P	108	Aide et al. 1995
60	M	A	116	Saldarriaga et al. 1988
60	M	A	197	Saldarriaga et al. 1988
60	M	A	138	Saldarriaga et al. 1988
80	M	A	134	Saldarriaga et al. 1988
80	M	A	178	Saldarriaga et al. 1988
80	M	A	144	Saldarriaga et al. 1988
80	M	A	142	Saldarriaga et al. 1988

Appendix 2. Soil C pools in forests of known age following tropical reforestation, and in nearby forests. Depth refers to soil depth of the measurement for soil C content. Soil 0–25 cm are the soil C values adjusted using a regression approach (see text). Life zones are wet (W), moist (M), and dry (D) based on author's descriptions. Past land uses are agriculture (A), pasture (P), or simply cleared and then abandoned (C). Cover types are secondary forests (S) or plantations (P).

Age yr	*Depth cm*	*Life Zone*	*Past Land Use*	*Cover Type*	*Soil C Mg/ha*	*Soil C 0–25 cm Mg/ha*	*Reference*
3	50	M	P	S	68	38	Buschbacher et al. 1988
4	30	W	A	S	116	94	Hughes et al. 1999
4	9	W	C	P	22	52	Lugo 1992*b*
5	40	M	A	S	78	53	Ramakrishnan & Toky 1981
5	10	W	P	S	14	30	Reiners et al. 1994
7	20	W	C	S	75	90	Williams-Linera 1983
8	50	M	P	S	65	37	Buschbacher et al. 1988
8	50	M	P	S	68	38	Buschbacher et al. 1988
8	50	M	P	S	70	39	Buschbacher et al. 1988
8	30	W	A	S	71	58	Hughes et al. 1999
8	30	W	P	S	120	98	Hughes et al. 1999
8	50	M	A	S	60	34	Kotto-Same et al. 1997
8	50	M	A	S	60	34	Kotto-Same et al. 1997
8	50	M	A	S	70	39	Kotto-Same et al. 1997
9	10	W	P	S	13	29	Reiners et al. 1994
9	10	W	P	S	19	40	Reiners et al. 1994
10	40	M	A	S	118	80	Ramakrishnan & Toky 1981
11	30	W	P	P	41	35	Cuevas et al. 1991
11	30	W	C	S	42	36	Cuevas et al. 1991
11	25	D	C	S	50	50	Brown & Lugo 1990*b*
12	25	W	A	P	72	72	Bashkin & Binkley 1998
12	10	W	P	S	21	45	Reiners et al. 1994
12	10	W	C	S	22	47	Reiners et al. 1994
15	40	M	A	S	98	66	Ramakrishnan & Toky 1981
15	10	W	C	S	21	45	Reiners et al. 1994
16	30	W	A	S	91	74	Hughes et al. 1999
16	30	W	P	S	77	66	Guariguata et al. 1997
16.5	30	W	P	S	79	68	Guariguata et al. 1997
17	30	W	P	S	114	98	Guariguata et al. 1997
17	12	W	C	P	40	74	Lugo 1992*b*
19	25	W	P	S	49	49	Lugo et al. 1986
20	30	W	A	S	102	83	Hughes et al. 1999
20	30	W	A	S	87	71	Hughes et al. 1999
23	50	W	A	S	90	51	Brown and Lugo 1990*b*
23	25	W	P	S	47	47	Lugo et al. 1986
23	20	M	C	P	117	141	Smith et al. 1998
26	50	M	A	S	70	39	Brown & Lugo 1990*b*
26	30	W	A	S	82	67	Hughes et al. 1999
30	30	W	A	S	117	95	Hughes et al. 1999
30	25	M	P	S	23	23	Lugo et al. 1986
35	25	D	A	S	75	75	Brown & Lugo 1990*b*
35	25	D	P	S	77	77	Lugo et al. 1986
36	20	M	C	P	92	111	Smith et al. 1998
36	20	M	C	P	93	112	Smith et al. 1998
36	20	M	C	P	95	114	Smith et al. 1998
40	50	M	P	S	90	51	Brown & Lugo 1990*b*
40	50	W	A	S	110	62	Brown & Lugo 1990*b*
40	25	W	P	S	60	60	Lugo et al. 1986
42.5	50	W	A	S	120	68	Brown & Lugo 1990*b*
49	7	W	C	P	22	62	Lugo 1992*b*
50	30	M	A	S	44	38	Greenland & Kowal 1960
50	25	D	A	S	90	90	Brown & Lugo 1990*b*
50	25	D	P	S	90	90	Lugo et al. 1986
50	40	M	A	S	103	69	Ramakrishnan & Toky 1981
55	50	M	A	S	145	82	Brown & Lugo 1990*b*

Continued

Appendix 2. Continued.

Age yr	*Depth cm*	*Life Zone*	*Past Land Use*	*Cover Type*	*Soil C Mg/ha*	*Soil C 0–25 cm Mg/ha*	*Reference*
61	10	M	P	P	40	86	Silver et al. 2001
100	50	M	A	S	152	86	Brown & Lugo 1990*b*
Mature	30	W			87	74	Guariguata et al. 1997
Mature	30	W			91	78	Guariguata et al. 1997
Mature	30	W			116	99	Guariguata et al. 1997
Mature	25	D			45	45	Brown & Lugo 1990*b*
Mature	25	D			60	60	Brown & Lugo 1990*b*
Mature	50	W			130	73	Brown & Lugo 1990*b*
Mature	25	W			62	62	Lugo et al. 1986
Mature	10	W			14	31	Reiners et al. 1994
Mature	10	W			17	36	Reiners et al. 1994
Mature	10	W			28	60	Reiners et al. 1994
Mature	20	M			106	128	Smith et al. 1998