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Publication Date

2014-05-01

DOI

10.1016/j.foreco.2014.01.024

Peer reviewed

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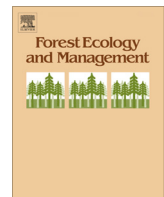
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Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Factors explaining variability in woody above-ground biomass accumulation in restored tropical forest



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ARTICLE INFO

Article history:

Received 12 December 2013

Received in revised form 16 January 2014

Accepted 20 January 2014

Available online 22 February 2014

Keywords:

Applied nucleation
Carbon sequestration
Costa Rica
REDD+
Soil C
Succession

ABSTRACT

Secondary forests comprise an increasing area of the tropics and play an important role in global carbon cycling. We compare above-ground biomass accumulation of both planted and naturally regenerating trees, as well as C in the top soil layer, in three restoration treatments replicated at 14, six to eight year old restoration sites in southern Costa Rica. Restoration strategies include: control (no planting), planting tree islands, and conventional, mixed-species tree plantations. We evaluate the importance of past land-use, soil nutrients, understory cover, and surrounding forest cover in explaining variation in above-ground biomass accumulation (ABA) rate across sites. Total ABA and planted tree ABA rate were highest in plantations, intermediate in islands, and lowest in control treatments, whereas ABA rate of naturally regenerating trees did not differ across treatments. Most ABA in plantations (89%) and islands (70%) was due to growth of planted trees. Soil carbon did not change significantly over the time period of the study in any treatment. The majority of across-site variation in both total and planted tree ABA rate was explained by duration of prior pasture use. Tree growth in the first two years after planting explained approximately two-thirds of the variation in ABA rate after 6–8 years. Soil nutrient concentrations explained relatively little of the variation in planted or naturally recruiting ABA rate. Our results show that planting trees substantially increases biomass accumulation during the first several years of forest recovery in former agricultural lands and that past-land use has a strong effect on the rate of biomass accumulation. Planting tree islands is a cost-effective strategy for increasing ABA and creating more heterogeneous habitat conditions than tree plantations. We recommend small scale planting trials to quickly assess potential biomass accumulation and prioritize sites for ecosystem service payments for carbon sequestration.

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1. Introduction

Secondary tropical forest cover is increasing rapidly in some regions, particularly in hilly, montane landscapes that are considered marginal for agriculture (Asner et al., 2009). This increase is due to both natural regeneration and active reforestation and restoration (Lamb, 2011; Aide et al., 2013). Given that tropical forest clearing comprises at least 12% of carbon emissions (van der Werf et al., 2009), there is an increasing focus on the role that forest recovery may play in sequestering carbon as part of efforts to reduce emissions from deforestation and forest degradation (REDD+, Edwards et al., 2010; Elias and Lininger, 2010; Harvey et al., 2010). This interest is clearly demonstrated by the large number of studies that have monitored the amount of C sequestered in both above-

ground biomass and soil carbon in both tropical forest plantations and naturally regenerating tropical forests (Bonner et al., 2013; Marín-Spiotta and Sharma, 2013; Martin et al., 2013).

Past studies show that the rate of above-ground biomass and soil C accumulation are highly variable at global and regional scales, which presents a challenge for predicting how much carbon can be sequestered as part of REDD+ programs and prioritizing areas to receive payments. Recent global scale meta-analyses indicate that differences in biomass and soil C accumulation are best explained by climate (primarily upland vs. lowland forests), total rainfall, soil type, and often past land-use (Silver et al., 2000; Paul et al., 2002; Cleveland et al., 2011; Bonner et al., 2013; Marín-Spiotta and Sharma, 2013).

Even at a relatively local scale many studies have shown high variability in tree growth, natural regeneration, and changes in soil C after land abandonment (Sarmiento et al., 2005; Sierra et al., 2007; Fonseca et al., 2012). Studies consistently show that

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above-ground biomass of both planted and naturally regenerating trees increases over time with particularly high rates of accumulation in the first 20 years post-abandonment (Silver et al., 2000; Marín-Spiotta et al., 2008; Bonner et al., 2013), but factors that explain differences in accumulation rates across sites in the same region vary. Intensity and duration of past land-use most commonly explain some of this variance (Uhl et al., 1988; Silver et al., 2000; Steininger, 2000; Letcher and Chazdon, 2009). Similarly, soil fertility explains differences in some cases (Carpenter et al., 2004a; Lawrence, 2005; Peña and Duque, 2013), but not in others (Feldpausch et al., 2004; Holl et al., 2011). Rules of thumb for predicting the variability in carbon sequestered across sites within a region remain elusive, which is partly due to the lack of well-replicated studies with data on baseline conditions.

An important question in designing strategies to enhance biomass and carbon accumulation in former agricultural lands is the relative effect of active restoration strategies, such as tree planting, compared to leaving land to regenerate naturally (Holl and Aide, 2011). Although a number of individual studies show that above-ground C accumulates faster in plantations than in natural regenerating sites (reviewed in Marín-Spiotta et al., 2008), a recent meta-analysis comparing monoculture tree plantations to natural regeneration sites across the tropics suggests that the effect of tree planting on above-ground biomass accumulation is weak and decreases with forest age (Bonner et al., 2013). Bonner et al. (2013), however, found few studies where natural regeneration and tree planting were compared in the same system and did not have sufficient studies of mixed-species tree planting to conduct a meta-analysis. Moreover, most past studies of both above-ground and soil C have relied on chronosequences rather than changes within individual sites over time, which can be problematic as they assume comparability of past land-use and other site conditions (Chazdon et al., 2007; Walker et al., 2010), and have been shown to overestimate biomass accumulation during the first several years of succession (Feldpausch et al., 2007).

Most past studies of tropical forest restoration have focused on tree planting using a mixture of native species. This commonly applied strategy accelerates forest recovery by encouraging animal seed dispersal, reducing cover of light-demanding pasture grasses, ameliorating microclimatic conditions, and enhancing nutrient availability (Chazdon, 2008; Lamb, 2011). Planting large areas of land with trees, however, can be costly (Lamb et al., 2005; Kanowski et al., 2008), and result in more homogeneous abiotic conditions than natural recovery (Holl et al., 2013). Moreover, the planted species selected can strongly influence biomass accumulation rates, nutrient cycling, and composition of naturally establishing species (Cusack and Montagnini, 2004; Celentano et al., 2011), particularly since fast-growing, low wood density species, including some N-fixers, are often selected for restoration plantings (Lamb, 2011).

Applied nucleation (i.e., planting trees in patches or islands) comprises an alternative hybrid forest restoration strategy between passive and plantation-style restoration that is less homogeneous and resource intensive (Rey Benayas et al., 2008; Corbin and Holl, 2012). This approach builds on observations that pioneer shrubs and trees naturally establish patchily in abandoned agricultural fields and facilitate the recruitment of other woody species via enhanced seed dispersal and improved establishment conditions (Yarranton and Morrison, 1974). The few experimental studies to date suggest that this strategy serves to enhance seed dispersal and seedling establishment in the first few years after planting (Robinson and Handel, 2000; Zahawi and Augspurger, 2006; Cole et al., 2010; Zahawi et al., 2013), but there have been no comparisons of woody biomass accumulation with other restoration strategies.

In this paper, we report on tree above-ground biomass accumulation (ABA) rate and soil C changes over the first 6–8 years of a well-replicated tropical forest restoration experiment. At each of 14 sites spread across a 100 km² area in premontane forest in southern Costa Rica, we established three restoration treatments: 1. Control – natural regeneration only; 2. Island – applied nucleation with six mixed-species tree islands; and 3. Plantation – planting the entire plot with the same mix of tree species. From the outset of the experiment we found highly variable rates of both planted tree growth and natural regeneration (Holl et al., 2011; Zahawi et al., 2013), and both the applied nucleation and plantation restoration strategies enhanced seed dispersal and seedling establishment compared to control plots (Cole et al., 2010; Zahawi et al., 2013).

Here we: (1) compare changes in both planted and naturally regenerating ABA rate in the three restoration treatments, and (2) investigate which factors best predict the variation across sites. Our aim is to provide information on the most promising restoration strategies and site prioritization criteria for enhancing ABA. We also report changes in soil C, but place less of an emphasis on this since past studies show that soil C changes tend to be small over the first 10 years of reforestation compared to above-ground changes (Paul et al., 2002) and generally do not show consistent correlations with forest age or differences in plantations vs. naturally regenerating lands (Marín-Spiotta and Sharma, 2013).

2. Methods

2.1. Study sites

We conducted this study at 14 sites separated by 0.7–8 km and located near the town of Agua Buena (8°44'36"N, 82°58'04"W) and the Las Cruces Biological Station (8°47'7"N, 82°57'32"W) in Coto Brus County, Costa Rica. Sites are in the tropical premontane rain forest zone (Holdridge et al., 1971), range in elevation from 1060 to 1437 m asl (Table S1), and receive mean annual rainfall ranging from 3 to 4 m with a dry season from December to March. Mean annual temperature is ~21 °C. Most sites are steeply sloping (15–35°) with a few on flatter terrain (5–10°). Sites span a range of aspects. Soils are volcanic in origin, including a mix of Andisols and Ultisols.

All sites had been used for ≥20 years for a mixture of agriculture (primarily coffee) and pasture although the length of usage for different agricultural activities varied across sites. Most sites were burned once or twice after clearing, but not thereafter. At the initiation of the experiment, sites were dominated by a mixture of pasture grasses (primarily *Axonopus scoparius*, *Pennisetum purpureum* Schumach., and *Urochloa brizantha* (Hochst. Ex. A. Rich.) R.D. Webster), forbs (mainly Asteraceae) and the fern *Pteridium arachnoideum* (Kaulf.) Maxon.

We collected information about the types and lengths of past land uses from landowners at the start of the study. We ranked the sites according to time since clearing and years of use as pasture, given that landowners could often only estimate dates to within a couple of years (Table S1). Sites with values within three years of each other were given the same ranking.

Like much of Central America, the landscape is a highly fragmented mosaic of mixed-use agricultural fields, pastures with fence lines that include trees, and forest patches. Forest cover within 500-m radius from the center of each plot was hand-digitized from orthorectified 2005 aerial photographs and spans a range from 9% to 89% (Cole et al., 2010).

2.2. Experimental layout

Each of the 14 sites were cleared of vegetation and divided into three 50 × 50 m plots which were assigned to one of three

treatments: control, island, or plantation (Holl et al., 2011). In plantation and island treatments, four tree species were planted; these included two timber species (*Terminalia amazonia* (J.F. Gmel.) Exell (Combretaceae) and *Vochysia guatemalensis* Donn. Sm. (Vochysiaceae)), and two fast-growing species that form N-fixing mutualisms and are commonly planted in coffee plantations in the region (*Erythrina poeppigiana* (Walp.) Skeels and *Inga edulis* Mart. (Fabaceae)). In the plantation treatment seedlings (20–30 cm tall) were planted in rows with 2.8-m separation throughout the entire plot (313 trees total). In the island treatment two small (5 trees), medium (13 trees), and large (25 trees) islands each were planted with a mixture of the four tree species at the same planting density as in the plantations. Islands were arranged in two rows with the order of island size randomized in each row. See Holl et al. (2011), Zahawi et al. (2013) for further experimental design details.

All vegetation beside the planted trees was cleared in all three treatments at ~3 month intervals using a machete or mechanical trimmer for 2.5 years to allow seedlings to grow above existing vegetation, after which sites were no longer managed. Sites were set up over three years (2004–2006), due to the large-scale of the study (6 sites planted in 2004, 5 in 2005, and 3 in 2006); but by three years after planting there was no significant effect of planting year on tree growth given the variability in growth rates across sites (Holl et al., 2011).

2.3. Data collection

2.3.1. Planted trees

We measured initial seedling height to the nearest 0.5 cm, and then recorded survival and height on an annual basis (June–July) for 3 years. Thereafter, we measured survival annually and diameter at breast height (DBH; 1.3 m) to the nearest 0.1 cm in alternating years. We recorded survival of all trees. We measured height and DBH of all trees in island plots and approximately one third of trees (randomly selected) in plantations to census an equal number of trees across planting designs. We used 2012 data (6–8 years after planting) for biomass calculations.

2.3.2. Natural recruitment

Naturally recruiting trees were sampled using a stratified layout with sampling area scaled to the size and distribution of age classes. We recorded DBH of tree saplings (≥ 1 and < 5 cm DBH) in 2×4 m quadrats ($N = 16$ Plantation (Pl)/Control (Co), $N = 30$ Islands (Is)); small trees (≥ 5 and < 10 cm DBH) in 8×8 m quadrats ($N = 4$ Pl/Co, $N = 8$ Is). Large trees (≥ 10 cm DBH) were surveyed in the interior 40×40 m plot area (5 m plot edge not sampled). We estimated percent cover of grasses, forbs, and bare ground in 1×1 m quadrats ($N = 16$ Pl/Co, $N = 30$ I) using a modified Braun-Blanquet cover-abundance scale: 0%, 1–5%, 5–10%, 10–25%, 25–50%, 50–75%, 75–95%, and 95–100% (Müller-Dombois and Ellenberg, 1974). The island treatment was sampled more intensively to quantify potential differences in recruitment between island interior and exterior, and among island sizes (Zahawi et al., 2013) but all measurements across treatments were standardized to a per hectare basis. When trees (either planted or naturally recruited) had more than one stem at 1.3 m, we measured the DBH of the three largest stems. We use tree recruitment data from 2013 sampling (4.5–6.5 years since clearing in plots ceased), and included herbaceous cover measurements from 6 to 7 mo after clearing ceased as a potential variable explaining differences in natural recruitment.

2.3.3. Soil

In August 2007 and July 2012 we collected 25, 2.5-cm diameter \times 15-cm deep soil cores across each plot. Cores were mixed, air dried, passed through a 2-mm sieve. In both years, samples

were analyzed for pH, Mehlich III P, and major cations using Mehlich III extractions following standard procedures at Brookside Laboratories, New Bremen, OH (see www.blinc.com/worksheet_pdf/SoilMethodologies.pdf and Gavlak et al., 2003 for details on protocols). In 2007, percent C and N from the same samples were determined by Dumas combustion using a Carlo Erba 1108 elemental analyzer at the University of California, Santa Cruz Stable Isotope Laboratory. For 2012 samples, percent C and N were quantified at Brookside Laboratories using an Elementar Vario EL Cube elemental analyzer. In 2008, we collected five soil bulk density cores (5-cm diameter \times 10-cm deep) across each plot. Samples were dried at 105 °C for ≥ 48 hr and weighed. We used soil %C and bulk density to calculate the change in bulk soil C between 2007 and 2012. We focused sampling on the uppermost soil layer where past work shows that C changes most rapidly (Guo and Gifford, 2002).

2.4. Statistical analyses

2.4.1. Biomass calculations

We calculated above-ground tree biomass accumulation (ABA) for all trees ≥ 1 cm DBH using the equation for moist tropical forests from Chave et al. (2005), based on the total rainfall and 3–4 mo dry season in our study region.

$$ABA_{\text{est}} = \rho \times \exp(-1.499 + 2.148 \ln(D) + 0.207(\ln(D))^2 - 0.0281(\ln(D))^3) \quad (1)$$

D is the trunk diameter (in cm) and ρ is the wood specific gravity (in g cm^{-3}). We used the model without tree height, as including tree height primarily improves models for large trees, where tree height increases have slowed (Vieilledent et al., 2011), which is not an issue in our early successional sites.

For common tree species in our plots (comprised $\geq 1\%$ of either the planted tree or naturally recruiting biomass) for which there were multiple published similar values in Central America in wood density databases (Chave et al., 2006; Zanne et al., 2009), we averaged published values. For common tree species where wood data were not available from multiple sites in Central America, we collected tree cores adjacent to our sites in July 2013; we calculated wood density following the protocol of Chave (2005) and using the water displacement method to measure volume (Table S2). For tree species that comprised $< 1\%$ of the naturally recruiting biomass, we used published values for the species when available and values for congeners in Central and South America when data were not available for that species.

We summed the ABA measurements of individual trees within a plot and converted values from the area sampled to per hectare values. We divided all values for ABA and Δ soil C by the number of years between measurements to calculate ABA on a per year basis (hereafter “ABA rate”), because our measurement intervals varied slightly according to when plots were initially set up and specific data were collected. To convert from ABA to above-ground Δ C for comparisons with other studies, we used a conversion factor of 0.48, based on data for broad-leaved tree species (including two that we planted) in the region (Arias et al., 2011); C values are usually slightly below 0.50 for early successional vegetation (Marín-Spiotta et al., 2008).

2.4.2. Treatment effects

All analyses were done using SAS 9.1.3 and we report means \pm 1 SD throughout. We inspected the distribution of the original data, as well as the residuals of our various models for normality and homogeneity of variance and some variables were arcsine square root (percentages) or log transformed.

The experiment was set up as a randomized complete block design with site as the blocking factor. We used a mixed-model

ANOVA to analyze the effect of treatment (fixed factor) and site (random factor) on planted tree, naturally recruiting tree, and total ABA rate, as well as Δ soil C. For planted tree ABA rate comparisons we only included plantation and island treatments. The landowner of one of our plots cleared all naturally recruiting vegetation after planted tree measurements but before natural recruitment sampling occurred in 2012 so that site was not included in natural recruitment and total ABA rate analyses.

We calculated the Spearman rank correlation coefficient between above-ground and below-ground carbon, and among abiotic variables. We used a *t*-test to determine whether Δ soil C in each treatment between 2007 and 2012 differed from 0. We also compared soil nutrient concentrations across treatments using a randomized complete block design.

2.4.3. Factors affecting variation across sites

We used stepwise regression with forward selection of variables to test the relative effects of treatment, soil nutrient concentrations (pH, Mehlich III P, total N, Mg, Ca, K, and percent base saturation), bulk density, land-use (ranked by time since land was originally cleared and duration of pasture use), understory vegetation (percent grass cover, forb cover, and bare ground), elevation, and percent surrounding forest cover at a 500-m radius on the variation in tree ABA rate and Δ soil C across sites. We used soil nutrient values from early in our experiment (2007) to assess the degree to which nutrient concentrations predicted tree growth. We used the GLMSELECT procedure in SAS and report all variables that entered the model at the $P < 0.05$ level, as well as identify those significant after approximate Bonferroni correction for multiple hypothesis tests ($P < 0.0031$). We checked for and did not find any collinearity of variables that entered the models.

We calculated height change (height in year n – initial height) through the third year at the plot level. We ran a regression with mean Δ tree height after 1, 2, and 3 yr as the independent variable and planted tree ABA rate over the 6–8 yr study period in island and plantation treatments as the dependent variable to determine the amount of variation explained by initial tree growth across sites.

3. Results

3.1. Treatment effects

Total tree ABA rate was highest in plantations, intermediate in islands and lowest in controls (Fig. 1, Table 1). Mean above-ground C sequestration rate was Plantation (PI) = $2.88 \pm 1.35 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, Island (Is) = 1.57 ± 0.96 , and Control (Co) = 0.40 ± 0.46 . Differences

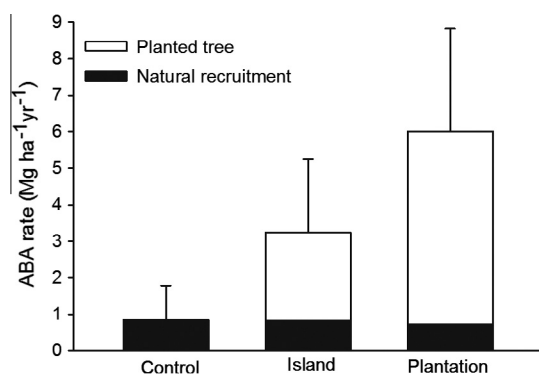


Fig. 1. Above-ground biomass accumulation in control, island and plantations treatments. Values are means \pm 1 SD. $N = 14$ per treatment for planted tree biomass and $N = 13$ for natural recruitment and total biomass.

Table 1

ANOVA models of above-ground biomass accumulation (ABA) rate and Δ soil C as a function of restoration treatment: Control (Co), Island (Is), Plantation (PI). Values with the same letter are not significantly different using a Tukey's test.

Variable	Df	F	p	Treatment		
				Co	Is	PI
Total above-ground ABA rate	2.24	46.3	<0.0001	a	b	c
Planted tree ABA rate	1.13	20.1	0.0006	– ^a	a	b
Planted tree ABA rate per tree	1.13	4.4	0.0552	– ^a	a	a
Natural tree recruit ABA rate	2.24	0.7	0.5160	a	a	a
Number of tree recruits >1 cm DBH	2.24	1.8	0.1892	a	a	a
Δ soil C	2.26	1.5	0.2445	a	a	a

^a Planted tree ABA rate was not compared in control treatments since no trees were planted.

in total ABA rate were driven by planted trees which accumulated 89%, 70%, and 0% of the annual above-ground woody biomass in plantations, islands and controls respectively. ABA rate resulting from planted trees was significantly higher in the plantation than island treatments (Fig. 1, Table 1) which is to be expected given that 3.6 times as many trees were planted in plantations. When planted tree ABA rate was divided by the number of trees planted in each treatment, however, per tree ABA rate was marginally higher in islands (Is = 6.8 ± 5.5 ; PI = $4.0 \pm 2.2 \text{ kg tree}^{-1} \text{ year}^{-1}$; Table 1). The range in planted tree ABA rate was large: plantations (1.04 – $9.36 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) and islands (0.23 – $7.03 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). Over half of the planted tree ABA rate resulted from *I. edulis* (52.0%) and a quarter from *V. guatemalensis* (25.2%); *E. poeppigiana* (12.6%) and *T. amazonia* (10.1%) contributed lesser amounts.

Similarly, ABA rate of natural recruits was highly variable: control (0.10 – $3.70 \text{ Mg ha}^{-1} \text{ yr}^{-1}$), island (0.01 – $1.89 \text{ Mg ha}^{-1} \text{ yr}^{-1}$), and plantation (0.05 – $5.08 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). Overall, neither ABA rate of natural recruits nor number of recruits >1 cm DBH was significantly different across treatments (Fig. 1, Table 1). The same result was found after excluding two outliers: one control plot had an ABA rate of $3.70 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (next highest was 1.19) and 70% of all recorded control recruits; and at a different site, a plantation plot had $5.08 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ (next highest 1.28) and 63% of the trees >10 cm DBH recorded in plantations. Between 2010 and 2012 (6–8 years after planting), the latter plot had high mortality of the planted species *I. edulis* with dying trees showing symptoms of a fungal infection; only 16% of *I. edulis* trees survived by 2012, as compared to an average of 88% survival across the other plots.

Forty-two species of tree seedlings of >1 cm DBH were recorded in plots, yet just 9 species contributed 92% of naturally recruiting ABA rate (Table S2). *Heliocarpus appendiculatus* constituted 50%; two species of *Cecropia*, two species in the Melastomataceae (*Conostegia xalapensis* and *Miconia theizans*), and *Lippia myriocephala* each made up 5–10%.

Δ Soil C in the top 15 cm did not vary across treatments (Table 1) and did not increase or decrease significantly between 2007 and 2012 ($t < 1.5$ and $P > 0.15$ for all treatments; Co: $-0.94 \pm 2.36 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, Is: -0.45 ± 0.156 , PI: 0.27 ± 2.27). As of 2012, C stored in the above-ground tree biomass comprised 3%, 18%, and 29% of the amount in the top 15 cm of soil for control, plantation, and island treatments respectively. Changes in total above-ground and soil C were not significantly correlated ($r = 0.03$, $P = 0.8464$). None of the major soil parameters varied across treatments early in the study (Table 2).

3.2. Factors affecting variation across sites

Restoration treatment and the length of pasture usage explained the most variation across sites in both planted tree ABA rate and total ABA rate (Fig. 2, Table 3). A relatively small amount (<15%) of variation in natural recruit ABA rate and Δ soil C were

Table 2
Soil nutrient concentrations and bulk density in restoration treatment plots in 2007. Values are mean \pm SD. $N = 14$ plots per treatment. Soil cores were 0–15 cm depth.

Soil variable	Control	Island	Plantation
Bulk density (g cm^{-3})	0.642 \pm 0.136	0.594 \pm 0.086	0.637 \pm 0.112
pH	5.54 \pm 0.19	5.57 \pm 0.24	5.54 \pm 0.25
Organic matter (%)	14.02 \pm 4.33	14.71 \pm 4.76	15.73 \pm 4.66
C (%)	7.18 \pm 2.41	6.80 \pm 2.29	7.46 \pm 2.79
N (%)	0.58 \pm 0.16	0.54 \pm 0.16	0.60 \pm 0.19
Mehlich III P (mg kg^{-1})	4.1 \pm 1.9	4.6 \pm 2.6	4.1 \pm 1.9
CEC ($\text{me } 100 \text{ g}^{-1}$)	12.59 \pm 4.45	14.78 \pm 7.13	13.83 \pm 8.42
Ca (mg kg^{-1})	1162.8 \pm 454.5	1458.2 \pm 832.6	1328.2 \pm 895.7
Mg (mg kg^{-1})	217.6 \pm 95.7	239.0 \pm 141.9	220.6 \pm 140.2
K (mg kg^{-1})	188.9 \pm 96.9	193.2 \pm 115.2	180.7 \pm 144.6
Na (mg kg^{-1})	30.5 \pm 10.1	37.3 \pm 2.3	35.6 \pm 4.8
Base saturation (%)	65.0 \pm 6.0	65.8 \pm 7.8	65.0 \pm 8.0

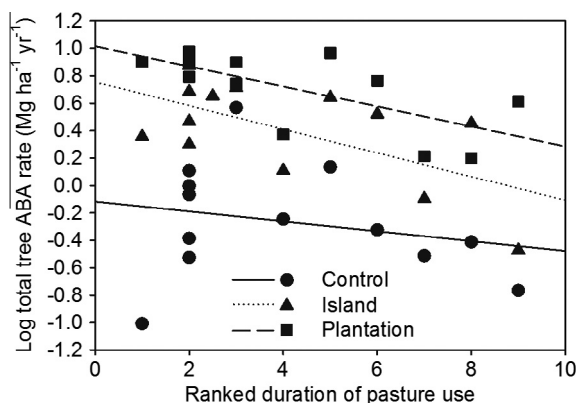


Fig. 2. Total planted tree above-ground biomass accumulation (ABA) rate as a function of restoration treatment and increasing duration of pasture use. $N = 13$ per treatment.

Table 3
Model selection parameters for variables explaining tree above-ground biomass accumulation (ABA) rate and Δ soil C. Variables are listed in the order they entered the model and adjusted r^2 values are for the model with the listed and previous variables included.

Response variable	Explanatory variable ^a	Model fit r^2_{adj}	p -Value ^b
Log (planted tree ABA rate)	Duration of pasture use	0.315	0.0011
	Treatment	0.534	0.0013
	N (%)	0.614	0.0197
Log (recruit ABA rate)	Log (extractable P)	0.123	0.0162
Log (total tree ABA rate)	Treatment	0.582	<0.0001
	Duration of pasture use	0.667	0.0029
Δ Soil C	N (%)	0.105	0.0209

^a Variables tested in the multiple regression model were restoration treatment, soil nutrient concentrations (pH, Mehlich III P, total N, Mg, Ca, K, and base saturation), bulk density, time since land was originally cleared, duration of pasture use, grass cover, forb cover, bare ground, elevation, and surrounding forest cover.

^b Bolded p -values indicate values that are significant ($p < 0.05$) after correcting for multiple hypothesis tests.

explained by soil nutrient concentrations; natural recruit ABA rate increased with extractable P, and total C with percent soil N. Length of pasture usage was weakly negatively correlated with K, but not correlated with any other soil nutrient concentrations or bulk density ($K: r = -0.29, P = 0.064$; all other nutrients and BD: $r < 0.16, P > 0.30$). Neither surrounding forest cover nor grass cover explained a significant amount of naturally recruiting ABA rate.

The increase in planted tree height by the second year explained approximately two thirds of the variation in planted tree ABA rate over the first 6–8 years (Fig. 3, Table 4). The percentage variation explained increased only slightly, particularly in islands, in the third year (Table 4). The amount of variation in ABA rate that was explained in plantations in years 2 and 3 was even higher when the one site with high mortality of *I. edulis* was excluded (year 2 height increase $r^2_{\text{adj}} = 0.776$, year 3 $r^2_{\text{adj}} = 0.814$).

4. Discussion and conclusions

4.1. Restoration treatment effects

Our results show that total tree ABA rate was highest in plantations, intermediate in islands, and lowest in control in the first decade after initiation of restoration treatments. This is not surprising given that the majority of ABA was comprised of planted trees. Growth rates of individual trees were slower in islands compared to plantation plots three years after planting (Holl et al., 2011). Our data after 6–8 years, however, show there was a trend towards higher biomass accumulation per tree in island plots. This suggests that planted tree growth in islands relative to plantations is increasing over time, which could be due to higher light conditions at island edges compared to the interiors of plantations as the trees mature (Riedel et al., 2013).

ABA rate of natural recruits >1 cm DBH was not significantly different across treatments. Results early in plot succession (2–5 years) showed that the number of tree seedlings recruiting was similar in plantation and island treatments and considerably lower in controls (Holl et al., 2013; Zahawi et al., 2013). But these differences were driven primarily by <1 -m tall tree seedlings. The largest natural recruits, which comprise the majority of ABA, likely established immediately after clearing ceased and before treatments were well developed. Moreover, tree seedlings have primarily established in locations where there is high canopy cover, which serves to increase seed rain and reduce competition with light-demanding pasture grasses (Cole et al., 2010; Holl et al.,

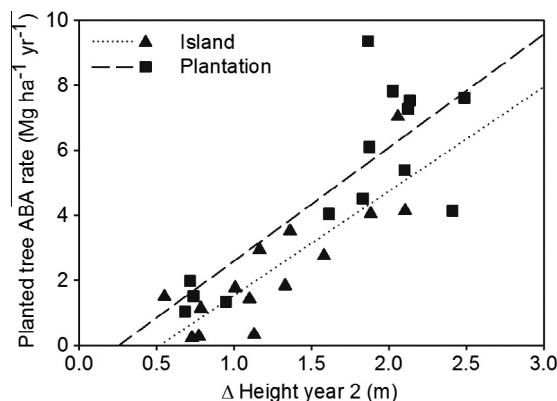


Fig. 3. Planted tree above-ground biomass accumulation (ABA) rate in years 6–8 accumulation as a function of height increase after two years. $N = 14$ per treatment.

Table 4
Regression of planted tree ABA rate on Δ tree height in the first three years in Plantation (Pl) and Island (Is) treatments.

	Pl r^2_{adj}	p	Is r^2_{adj}	p
Δ Height – year 1	0.402	0.0088	0.220	0.0519
Δ Height – year 2	0.629	0.0004	0.691	0.0001
Δ Height – year 3	0.646	0.0003	0.805	<0.0001

2013). The low light conditions, however, substantially reduce seedling growth (Loik and Holl, 1999; Celis and Jose, 2011), so these seedlings contribute little to overall biomass over the short-term but are likely to grow rapidly when the planted trees senesce.

Our values for planted tree ABA rate and, particularly, naturally regenerating tree ABA rate are at the low end of the wide range of values that have been reported in the literature (Lugo, 1988; Silver et al., 2000; Bonner et al., 2013). Our planted tree ABA rate values are approximately half of those reported for single species plantings of *Terminalia amazonica* and *V. guatemalensis* in the lowlands of Costa Rica (Redondo-Brenes, 2007; Fonseca et al., 2012); however, these authors measured single species plantations managed for forestry. The slower planted tree and natural recruitment growth compared to values from others studies is likely related to the fact that our sites are in premontane forest where biomass accumulation rates are lower than in lowland sites (Cleveland et al., 2011), and all sites had lengthy prior agricultural use.

Our results concur with a large amount of past literature showing that tropical soils comprise the largest C pool, particularly early in succession (Russell et al., 2010; Fonseca et al., 2012). We did not observe any changes over time nor effects of our different restoration treatments on soil C. This result is not surprising given (1) the relatively short interval of time between our measurements (five years); (2) the fact that soil C changes more slowly than above-ground biomass, particularly in higher elevation rain forests (Paul et al., 2002; Marín-Spiotta and Sharma, 2013; Martin et al., 2013); and (3) the large size of the existing C pool makes it difficult to detect changes (Marín-Spiotta et al., 2008). Past reviews have reported inconsistent changes in soil C with transitions from pasture to broad-leaved tree plantations (Guo and Gifford, 2002; Martin et al., 2013). This may be due to the fact that pasture grasses, which are shaded out in plantations and secondary forests, can have a strong positive effect on soil C (Silva et al., 2013).

4.2. Factors affecting variation across sites

We, like many previous studies, show high variability in both planted tree growth and natural recruitment across sites (Aide et al., 2000; Redondo-Brenes, 2007; Sierra et al., 2007; Manson et al., 2013). Past land-use, specifically duration of pasture use, was the best predictor of planted tree ABA rate and in turn total ABA rate. Similarly, many past studies show that longer use of land, and in particular, use for pasture as compared to other agricultural crops, slows biomass accumulation (Hughes et al., 1999; Silver et al., 2000; Steininger, 2000; Lawrence, 2005). Although some studies do not show such an effect (Steininger, 2000; Peña and Duque, 2013), intensity of past land use seems to be the most consistent factor affecting the rate of tropical forest recovery (Silver et al., 2000; Marín-Spiotta et al., 2008; Bonner et al., 2013).

Long-term pasture usage can affect tree growth through changes to soil nutrient concentrations, erosion, and compaction, as well as to the soil biota (Buschbacher et al., 1988; Carpenter et al., 2001; Cleveland et al., 2003). Interestingly, in our study, duration of pasture use was not strongly correlated with any soil physical or chemical variables, although it is possible that there may be differences in compaction or soil nutrient concentrations at greater soil depths that were not analyzed. Another possibility is that long pasture usage affected microbial communities; increasing intensity of past land use can substantially affect biotic communities including microbes, mycorrhizae and potentially root herbivores (Carpenter et al., 2001; Melo et al., 2012; Araujo et al., 2013).

A considerable amount of the variability in above-ground biomass of planted trees 6–8 years after planting was predicted by change in tree height after only two years. Similarly, other research

in former pastures suggests that ranking tree seedling performance across species in the first 1–2 years can predict performance over the next few years (Martínez-Garza et al., 2013; Riedel et al., 2013). Longer-term data will help to assess whether our trend in comparative biomass accumulation across sites will hold, but this result suggests that small-scale tree planting trials may be highly valuable to inform where to invest money in larger-scale plantings when resources are limited (Holl and Aide, 2011; Martínez-Garza et al., 2013).

Soil nutrient concentrations explained only a small amount of the variation in natural recruitment and planted tree biomass. Past correlative studies of natural regeneration and tree growth have shown highly mixed effects of nutrients on tree growth and biomass (Lawrence, 2005; Manson et al., 2013; Peña and Duque, 2013). But, chronosequence studies typically do not have baseline soil nutrient data, and current tree growth both affects and is influenced by soil nutrient concentrations making it impossible to tease out cause and effect. Soil nutrient concentrations in the tropics vary of small spatial scales (Townsend et al., 2008; Holl et al., 2013); so measurements of soil nutrients at smaller spatial scales than our plots (50 × 50 m) might better predict tree growth, but are not practical to collect over large areas. Fertilization studies in the tropics have shown evidence of N, P, and K limitation of tree growth and biomass accumulation in most but not all cases, although the primary limiting nutrient varies (Lawrence, 2003; Carpenter et al., 2004b; Ceccon et al., 2004; Santiago et al., 2012). Regardless, the lack of consistency in the significance in correlations between soil nutrient concentrations and either tree growth rates or total ABA rate make commonly measured indicators of soil fertility (e.g. pH, extractable P and cations) an unreliable predictor of carbon sequestration potential. Labile nutrients cycle quickly in tropical forests so nutrient fluxes or microbial community composition and activity may be better predictors of nutrient availability (Vandecar et al., 2009; Araujo et al., 2013), but land owners and managers rarely have access to such information.

Little of the variation in natural recruitment across sites was explained by measured factors. In most abandoned agricultural lands, including our sites, natural recruitment is highly dispersal limited (reviewed in Holl, 2002; Chazdon, 2003; Kettle, 2012), so we had anticipated that naturally recruiting ABA rate would increase with surrounding forest cover, consistent with results of a recent meta-analysis (Bonner et al., 2013). The lack of surrounding forest cover effect is likely due to the fact that the most common early colonizing species in our plots, such as *Cecropia* spp., *H. appendiculatus*, and various tree species in the Melastomataceae, are widespread as remnant trees and along fence lines in the landscape (Cole et al., 2010). We were surprised that herbaceous cover early in the study did not explain variation in natural recruitment biomass, as pasture grasses in particular compete strongly with young seedlings (Hooper et al., 2005; García-Orth and Martínez-Ramos, 2011); however, once trees grow taller than the grasses they rapidly shade out the light-demanding grasses so competition is reduced.

4.3. Management recommendations

Our results and many other studies show that actively planting trees substantially accelerates above-ground biomass accumulation compared to natural recovery in the first decade or two compared to natural regeneration (Omeja et al., 2011; Bonner et al., 2013; Wei et al., 2013), particularly in upland forests and when past land-use has been more intense. Comparisons of data from different sites suggest that these ABA rate differences tend to converge after two decades (Jordan and Farnworth, 1982; Bonner et al., 2013), but there are few long-term data of contrasting restoration approaches from within the same sites to confirm this trend.

Such data are needed to evaluate whether the added costs of tree planting enhance biomass accumulation over the long-term (Jordan and Farnworth, 1982). We planted mostly fast-growing, low wood density species, like many forest restoration projects, and, as would be expected, the initial recruiting trees largely shared these traits. Others have suggested that a better investment may be enrichment planting with large-seeded, slower growing species (Martínez-Garza and Howe, 2003; Lamb et al., 2005) to achieve goals of both carbon sequestration and biodiversity conservation over the longer-term.

Although traditional plantation-style tree planting restoration approach resulted in higher biomass accumulation this is only one measure of forest recovery. The tree island (applied nucleation) restoration strategy also enhanced biomass accumulation over natural regeneration, albeit to a lesser extent. It is a cheaper restoration strategy (Holl et al., 2011) that results in more heterogeneous habitat conditions and less legacy effects of planted trees on nutrient cycling (Celentano et al., 2011; Holl et al., 2013). These differences, along with the time frame for evaluating success, need to be weighed in selecting an appropriate restoration strategy.

Tropical forest restoration has been heralded as a potential win-win situation to reduce net carbon emissions and erosion, as well as to increase biodiversity (Elias and Lininger, 2010; Harvey et al., 2010). In addition, there is the potential for funding through REDD+ voluntary payments or bi-national agreements. However, with such broad ranges in ABA across sites, it becomes challenging to accurately estimate the amount of carbon that will be sequestered through reforestation and forest regeneration efforts in a given region. Our results highlight the importance of placing a first priority on protecting intact forest, given the uncertainties involved in forest recovery, as well as the need for ways to reduce this uncertainty. Setting up small-scale tree planting test plots and monitoring natural recovery in former agricultural lands for even a couple of years is a wise investment to determine how to best allocate restoration resources before implementing a large-scale project (Holl and Aide, 2011).

Acknowledgements

We are grateful for help in the field from J.A. Rosales, P. Rosales, J. Hidalgo, and many students and Earthwatch volunteers. We thank R. Ostertag, M. Bonner, and two anonymous reviewers for helpful feedback on earlier drafts of this paper. Financial support for this project was provided by NSF (DEB 05-15577; DEB 09-18112), and the Earthwatch Foundation. We greatly appreciate the various landowners providing access to their lands.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.01.024>.

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