



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



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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), but a few studies have shown no effect (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

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