Ecological Applications, 0(0), 2019, e01847

Intensive silviculture enhances biomass accumulation and tree diversity recovery in tropical forest restoration

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Citation: Brancalion, P. H. S., O. Campoe, J. C. T. Mendes, C. Noel, G. G. Moreira, J. van Melis, J. L. Stape, and J. Guillemot. 2019. Intensive silviculture enhances biomass accumulation and tree diversity recovery in tropical forest restoration. Ecological Applications 00(00): e01847. 10.1002/eap.1847

Abstract. Maximizing initial aboveground woody biomass (AGB) accumulation in order to obtain early payments for carbon stocking is essential for the financial viability of reforestation programs fostered by climate mitigation efforts. Intensive silviculture, i.e., silviculture traditionally used in commercial forestry to maximize productivity and gains, has recently been advocated as a promising approach to enhance AGB accumulation in restoration plantations. However, this approach may hamper natural forest regeneration and ecological succession due to high competition between colonizing plants and planted trees. We investigated the impacts of different silvicultural treatments applied to restoration plantations with 20 native tree species on AGB accumulation and spontaneous regeneration of native woody species in an experiment set up in the Atlantic Forest of Brazil. Intensive silviculture demonstrated a remarkable potential to enhance AGB accumulation in restoration plantations by increasing up to three times the AGB of tree stands (from ~25 to 75 Mg/ha in the 12th year). Intensive fertilization/weed control enhanced AGB accumulation, while higher tree density and the proportion of pioneers did not have a significant effect on AGB over the time. In spite of higher costs (cost increase of 13–19%), the cost-effectiveness for AGB accumulation of intensive silviculture was comparable to that of traditional silviculture applied to restoration (US$50–100/Mg AGB for 3×2 m spacing). Contrary to our expectations, we did not find a trade-off between AGB accumulation by planted trees and the spontaneous regeneration of tree species, since intensive silviculture enhanced the regeneration of both planted (total of 12 species) and colonizing woody species (total of 30 species) in the plantation understory. Specifically, a strong association was found between AGB stocks and the abundance and richness of colonizing species, a vast majority of which (90% of species and 95% of individuals) were dispersed by animals. We report a case of positive correlation between AGB stocking and woody species regeneration in the restoration of the Atlantic Forest. Fostering the establishment and maintenance of restoration tree plantations can, in some cases, be a win-win strategy for climate mitigation and biodiversity conservation in human-modified tropical landscapes.

Key words: Atlantic Forest; carbon accumulation; cost-effective silviculture; natural regeneration; restoration plantations; silvicultural management; tropical forestry.

Introduction

There is a growing global recognition of the key role of forest restoration in mitigating climate change (Harris et al. 2006, Bonan 2008, Feng et al. 2013, Griscom et al. 2017). International commitments on forest landscape restoration have accumulated pledges to restore over 160 million hectares, 82% of the area being located in tropical regions (Chazdon et al. 2017, Holl 2017). Forest-based climate mitigation emerged as a key component of the recent Paris Climate Agreement (Grassi et al. 2017), which confirmed the ongoing political momentum for promoting reforestation and forest restoration. While tropical deforestation has substantially contributed to the increase of atmospheric CO_2 in recent decades (Zarin 2012), the accumulation of biomass in reforested or restored tropical areas is widely considered as a major tool for future climate change

Manuscript received 24 May 2018; revised 16 October 2018; accepted 13 November 2018. Corresponding Editor: Yude Pan.
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mitigation (Alexander et al. 2011, Hulvey et al. 2013, Locatelli et al. 2015, Chazdon et al. 2016, Brancalion et al. 2018).

The gross primary production of tropical forests is among the highest in the world (~40.8 Pg C/yr; Beer et al. 2010) and largely contribute to the current terrestrial carbon sink (Pan et al. 2011, Phillips and Lewis 2014). However, second-growth forests take at least several decades to recover predisturbance biomass levels (Martin et al. 2013, Poorter et al. 2016), which is in stark contrast to carbon markets that operate on a shorter timeframe. For instance, afforestation and reforestation projects included in the Clean Development Mechanism, established by the Kyoto Protocol to allow industrialized countries to invest in emission reduction or sequestration of greenhouse gases in developing countries, can generate carbon credits for a limited period of 30 yr (Thomas et al. 2010). Maximizing initial biomass accumulation in order to obtain early payments for carbon stocking is therefore essential for the financial viability of reforestation programs where costs are concentrated in the first few years of implementation (Brancalion et al. 2017).

Intensive silviculture, i.e., silviculture traditionally used in commercial forestry to maximize productivity and gains, has been advocated as a promising approach to enhanced biomass accumulation and efficiency in young restoration plantations (Campoe et al. 2010, Ferez et al. 2015). Intensive silviculture guidelines include the use of fast-growing species to reach early canopy closure, soil preparation to promote root growth and optimize resources acquisition, soil fertilization to avoid nutrient limitations on tree growth, and chemical weed control to eliminate competition with undesirable plants (Goncalves et al. 2013). These treatments improve the physiological performance of native trees, leading to higher initial survival and growth (Campoe et al. 2014). Intensive silviculture may, however, hamper natural forest regeneration and ecological succession if planted trees rapidly dominate the system and use most of the environmental resources available at the site. Natural regeneration of spontaneously regenerating plants is considered a key ecological process for tropical forest restoration success (Suganuma and Durigan 2015, Viani et al. 2015, Wheeler et al. 2016), and impeding it has serious negative consequences for the ecological sustainability of restored forests (Parrotta et al. 1997, Martínez-Ramos et al. 2016, César et al. 2018).

Forest tree diversity and carbon stocks show limited correlation in tropical forests worldwide (Sullivan et al. 2017, Marco et al. 2018), implying that both carbon and diversity aspects should be explicitly considered in the design of silvicultural guidelines and forest policies. For example, restoration plantations in Costa Rica showed higher aboveground biomass accumulation than tree islands, but the latter tree planting strategy resulted in more heterogeneous habitat conditions, which better supports regeneration processes (Holl and Zahawi 2014). An alternative restoration approach consists in planting fast-growing, exotic tree species to maximize biomass accumulation and wood supply while promoting natural regeneration of native species in the plantation understory (Janzen 2000, Lamb et al. 2005, César et al. 2018). Carbon-centered restoration is indeed considered to be a risk for biodiversity conservation in many region of the world, notably through the use of exotic species, afforestation of native grasslands, alteration of natural disturbance regimes, and clearing of native vegetation to establish tree plantations (Lindenmayer et al. 2012, Brancalion and Chazdon 2017). To the best of our knowledge, the effect of carbon-centered intensive silviculture on the abundance and species diversity of spontaneous regeneration in native tropical plantations remain unexplored.

We investigated the impacts of different silvicultural treatments applied to restoration plantations with native trees on biomass accumulation and spontaneous regeneration of native woody species. We hypothesized that more intensive silviculture would lead to higher biomass accumulation, but lower abundance and diversity of spontaneously regenerating plants due to lower resources availability in the understory of carbon-richer plots, thus evidencing a trade-off between carbon stocking and the biodiversity value of restored forests. We further explored the ecological processes through which aboveground biomass influences native species regeneration in plantation understory.

Methods

Study site

The experiment is located at the Anhembi Experimental Station of Forest Sciences, University of São Paulo, Anhembi-SP, southeastern Brazil (22°40′ S, 48°10′ W). Elevation is 455 m above sea level, relief is flat (<5%), climate is classified as mesothermic Cwa (Köeppen classification system; Alvares et al. 2013) with a mean annual temperature of 19°C, wet and warm summers, dry and cold winters, annual precipitation of 1,170 mm and annual water deficit of 20 mm. Soil is characterized as acid (pH 4.0), Yellow Distrophic Latossols (Embrapa 2006), with low nutrient content (organic matter: 20 g/dm^3; P: 7 mg/dm^3; K: 1.1 mmol$_c$/dm^3; Ca: 7.0 mmol$_c$/dm^3; Mg: 4.0 mmol$_c$/dm^3; cation exchange capacity: 38.1 mmol$_c$/dm^3) and sandy texture (5% silt, 13% clay, and 82% sand).

This region was once dominated by semideciduous seasonal forest, the major forest type covering inland regions of the Atlantic Forest biome, a global hotspot for biodiversity conservation (Morellato and Haddad 2000, Myers et al. 2000). This is also the dominant forest type within the “interior” biogeographical region of this biome, the second most threatened with only 7% of remaining forest cover (Ribeiro et al. 2009). Native forest cover was drastically reduced in the early 20th century in the Anhembi region for expanding coffee plantations, which was later replaced by extensive pasturelands and plantations of sugarcane, eucalypt, and citrus (Dean 1995). In 1974, when the experimental station was established, the conditions for natural regeneration of native woody plants were very limited, since the station is surrounded by a large water reservoir and there was only one small forest fragment remaining in the landscape (Fig. 1A). Regeneration conditions were subsequently enhanced by increasing soil matrix permeability through the establishment of exotic tree woodlots and restoration plantations in the riparian buffers of the reservoir (Fig. 1B).

Experiment set-up

The experiment was set up in 2004 in a pasture area covered by the exotic African grass *Urochloa decumbens* (Stapf) R.D. Webster, the major fodder grass used in Brazil and also the most important target of weed control in the restoration plantations of the region (Brancalion et al. 2016b). No native trees were regenerating at the site by the time of the experiment implementation. Grasses were initially controlled by spraying 5 L/ha of glyphosate, and planting rows were opened with a subsoiler at 40 cm depth once grasses were fully desiccated.

We established a 2 × 2 × 2 full factorial experiment to isolate the effects of the most frequent features of intensive silviculture guidelines on biomass accumulation and species regeneration. Specifically, three factors were manipulated (abundance of fast-growing tree species, density of individuals, and soil fertilization/weeding), each of them having two levels, which resulted in eight contrasted treatments. The experiment was implemented in a randomized block design with four replicates, in 42 × 30 m plots (1,260 m^2; Fig. 1C).

- In factor 1, the proportion of pioneer trees is 50% pioneer : 50% non-pioneer for level 1 and 67% pioneer : 33% non-pioneer species for level 2. A total of 20 native tree species was used (10 pioneers and 10 non-pioneers, the same density of individuals per species was used in all treatments; Appendix S1), whose successional classification was based on interviews with restoration practitioners and forest nursery managers (Campoe et al. 2010);
- In factor 2, the density of individuals is 3,333 trees/ha (3 × 1 m planting spacing) for level 1 and 1,666 trees/ha (3 × 2 m planting spacing) for level 2. Planting lines were prepared with a subsoiler every 3 m and seedlings were distributed along the lines every 1 m (level 1) or 2 m (level 2);
- Factor 3 deal with fertilization and weed control. Two levels of silvicultural treatment were obtained by using the interventions applied in typical restoration plantations of the region: level 1 (hereafter referred

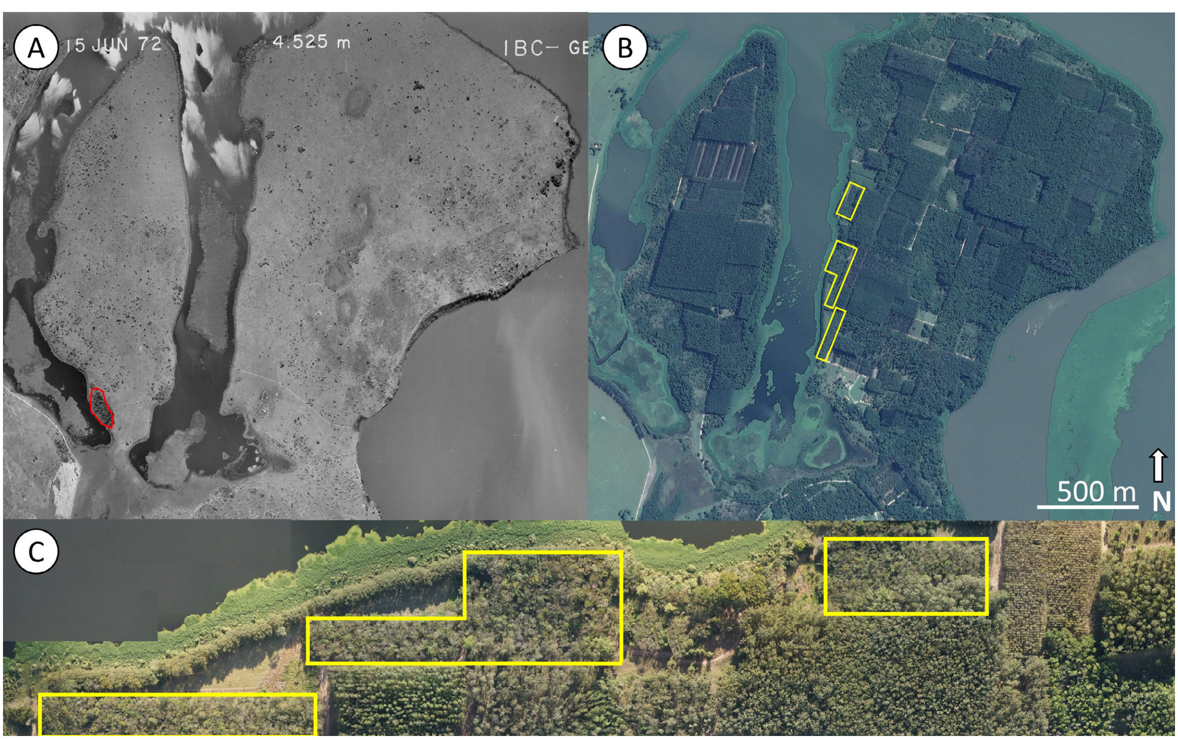

Fig. 1. Aerial images of the Experimental Station of Anhembi, Brazil in (A) 1972 and (B) 2018 and (C) of the experiment. The red polygon in the left lower corner of image A evidences the only forest remnant remaining in the landscape, and the polygons at the center of images B and C highlight the experiment area.

as “usual fertilization/weed control”), which uses repeated weeding in a 50 cm width strip in planting rows and mechanized chopping between rows at 6, 12, 18, and 24 months after planting, and fertilization with 27 kg N, 21 kg P, 11 kg K, and 24 kg Ca per hectare, distributed as one single basal fertilization and two broadcasting fertilizations in the second and third year with NPK 18-06-24, and level 2, which increases the addition of fertilizers and using more effective weeding treatments (hereafter referred as “intensive fertilization/weed control”) by repeated spraying with 5 L/ha of glyphosate to control weeds across the entire plot every 3 months until canopy closure (first 2 yr), and fertilization with 81 kg N, 62 kg P, 33 kg K, 452 kg Ca, and 180 kg Mg per hectare, which is three times the total amount used in level 1, distributed as one single basal fertilization and two broadcasting fertilizations in the second and third year with NPK 18-06-24 (Campoe et al. 2010). The total establishment costs for three years of the studied restoration plantations were, for the usual tree density (1,666 trees/ha) 4,194 US$/ha and 4,990 US$/ha under usual and intensive fertilization/weed control, respectively (Appendix S1).

The level 1 of factors 1, 2, and 3 described above represent the traditional silvicultural guidelines used in restoration plantations in the Atlantic Forest (Rodrigues et al. 2009). In order to minimize edge effects, the external planting line of each plot was considered as a buffer area, resulting in a 36 × 22 m (792 m^2) effective area per plot. All the costs involved in the establishment of silviculture treatments were recorded during the implementation and maintenance of the experiment (Appendix S1). The cost of pioneer non-pioneer seedlings did not differ.

Field measurements

Aboveground woody biomass.—An allometric equation ($r^2 = 0.94$; $P < 0.0001$) was developed based on species-specific wood density measurements, and dendrometric and destructive biomass measurements of four trees per species (total of 80 trees) when the plantation was five years old (Ferez et al. 2015):

$$\ln(\mathrm{AGB_W}) = 6.039 + 0.945 \times \ln(\mathrm{SA}) + 0.961 \times \ln(\mathrm{Ht}) + 1.022 \times \ln(\rho)$$

in which AGB_W is woody aboveground biomass (kg); SA is basal area, measured at bole diameter (0.3 m above ground level; m^2); Ht is height (m); ρ is wood specific gravity (g/cm^3).

We applied this equation to forest inventories performed yearly over the 2006–2016 period (except in 2014) to assess the aboveground woody biomass (AGB) of each experimental plot. The basal area of each tree was obtained from bole diameter measured at 0.3 m above ground level, and total height of each tree was measured using an electronic clinometer.

Woody species regeneration in the understory and ground cover by grasses and litter.—We implemented eight 3 × 3 m subplots within each study plot, which covered 10% of the effective plot area. Subplots were implemented in a systematic grid design to maximize the spatial representation of the plot. All regenerating individuals of woody species taller than 50 cm were inventoried and identified to species level in the summer of 2016. Regenerating individuals were separated into “planted species” (i.e., the 20 species planted in the experiment), and “colonizing species” (i.e., species not planted in the experiment). The seed dispersal syndrome of identified “colonizing species” (i.e., biotic- and abiotic-dispersed) was determined according to Bello et al. (2017). The same subplots were used to assess ground cover by *U. decumbens*, using a 1 × 1 m wood frame subdivided into 100 0.1 × 0.1 m grids and positioned at the center of the subplot. We wanted to evaluate grass ground cover as a continuous variable, but since 94% of the subplots had 100% or 0% of their area covered by grasses, we analyzed presence (>10% ground cover) or absence (<10% grass cover) of grasses in the subplots as a discrete variable. Grass cover data were collected in the wet season of 2016. In addition, we established a 0.5 × 0.5 m frame at the center of each subplot and collected litter deposited on the ground in the wet season of 2016 and in the dry season of 2017. Litter layer samples were carefully checked for soil particles, oven-dried at 80°C for 72 h, and weighed.

Light interception by the canopy.—We assessed the percentage of photosynthetically active radiation intercepted by the canopy (iPAR, wavelength from 400 to 700 nm) at the center of each of the regenerating vegetation subplots. A ceptometer AccuPAR LP-80 (Decagon Devices, São José dos Campos, SP, Brazil) was used inside the plots for below canopy measurements, and another was kept in an open area nearby, to measure incoming PAR. The latter was logged to measure PAR every minute, and each measurement was paired to the PAR obtained at the same moment below canopy to calculate the iPAR of each sampling point. Intercepted PAR was measured in the dry season of 2017 and in the wet season of 2018.

Data analysis

Effects of silviculture guidelines on aboveground woody biomass and woody species regeneration.—We performed linear mixed-models analysis in order to test for the effects of the three studied silvicultural factors on AGB accumulation in our experiment. First, we performed three independent mixed-models analyses where one of the three studied silvicultural factors was included with a fixed effect. These three fixed factors stood for the effects of (1) fertilization inputs/weed control (intensive vs. usual fertilization/weed control); (2) density of trees (3,333 vs. 1,666 ind./ha); and (3) proportion of pioneers (67:33 vs. 50:50 proportion of pioneers : non-pioneers). Age of plantation (2005–2016: 14 measurements) was included as a covariate in all three models and plot ID was considered a random effect due to the repeated measurement design. When the main effects of more than one fixed factor were significant ($P < 0.01$), we explored their interactions using them as fixed factors, time as covariate and plot ID as random factor in another linear mixed model. The dependent variable aboveground biomass (AGB) was log-transformed to meet the assumptions of the tests. Similarly, we built linear mixed models in order to perform post hoc analyses of the differences in biomass increments over time among the various studied treatments (i.e., differences in the AGB × time slopes). We finally evaluated the cost-effectiveness of the silvicultural treatments by calculating the ratio between biomass accumulation and total cost when the plantation was 12 yr old. Analyses were conducted using the lmer and lstrend functions from the lme4 (Bates et al. 2015) and lsmeans (Lenth 2016) R packages.

In order to assess the effect of the three two-level categorical variables on woody species regeneration, we performed generalized linear models with a Poisson error structure to estimate the signal of the estimated coefficients and their significance ($P < 0.01$). Then we assessed if the (1) proportion of pioneers (67:33), (2) fertilization inputs/weed control (intensive), or (3) tree density (3,333 ind./ha) has a positive or negative significant effect on number of individuals and number of species regenerating in the plantation understory. We conducted these analyses separating "colonizing" and "planted" species. Residuals overdispersions of our models were analyzed following Zuur et al. (2009).

Association between aboveground woody biomass and woody species regeneration in the plantation understory.—Generalized linear models with a Poisson error structure were used to evaluate the effect of AGB on woody species regeneration. Two important features of species regeneration were specifically studied: species richness (number of species per plot) and the total sum of individuals (abundance). "Planted" and "colonizing" species regeneration were considered separately in the analyses. We used pseudo-R^2 of McFadden as a coefficient to assess the explanatory power of our models.

Drivers of woody species regeneration in the understory.—Structural Equation Models (SEM) are well suited for testing and quantifying indirect or cascading dependences in complex systems (Grace et al. 2010). The principle of SEM is to confront available a priori knowledge of interacting variables to data in order to retrieve a realized dependence matrix. We therefore built a priori hypotheses regarding the expected effects of plantation characteristics (basal area of planted trees, iPAR, grass incidence, and litter mass) on the density and richness of colonizing woody species. Since regular SEM use a covariance matrix to determine a global estimator, they rely on the assumption that variables follow normal distribution (Grace et al. 2010), which prevents their use for count (Poisson distribution) data or binary (binomial distribution) data. We therefore used the piecewiseSEM R package (Lefcheck and Freckleton 2016) to perform and analyze our SEM models (see Appendix S1 for R script), because piecewise SEM uses localized estimators, allowing Poisson and Binomial distributions (Grace et al. 2010, Lefcheck and Freckleton 2016). Model fit was assessed using Fisher's C statistic, where $P > 0.05$ indicates that the data are well represented by the model.

Results

Effects of silviculture guidelines on aboveground woody biomass

Differential silviculture approaches resulted in plantations with remarkably different ABG stocks at the 12th year after planting (ranging from ~25 to 75 Mg/ha; Fig. 2). Intensive fertilization/weed control enhanced AGB accumulation, while higher tree density and the proportion of pioneers did not have a significant effect on AGB over time (Fig. 2; Table 1). The relative increase of AGB overtime was higher in the usual fertilization/weed control plots ($\text{slope}_{\text{usual}} = 0.30$ [0.28–0.33, 95% confidence interval]; $\text{slope}_{\text{intensive}} = 0.24$ [0.21–0.26]), and at lower tree density ($\text{slope}_{\text{lower density}} = 0.29$ [0.27–0.32]; $\text{slope}_{\text{higher density}} = 0.25$ [0.22–0.27]). However, AGB remained higher in the intensive fertilization/weed control ($F_{30,1} = 19.99$; $P < 0.0001$) and denser ($F_{30,1} = 8.43$; $P < 0.0069$) plots 12 yr after planting. Fertilization/weed control interacted with tree density on AGB ($F_{28,1} = 7.44$; $P = 0.01$), but a significant impact of fertilization/weed control management was only observed at lower tree density ($P < 0.0001$), with a positive effect of intensive fertilization/weed control on AGB. Growth performance of trees was enhanced by intensive fertilization/weed control and reduced by high tree density for most species, and the reduced proportion of pioneers had also a positive effect on fast-growing species (Appendix S1). In spite of higher costs, the cost effectiveness for AGB accumulation of intensive silviculture was comparable to that of traditional silviculture applied to restoration, whereas the cost effectiveness of denser plantations was much lower (Fig. 3).

Effects of silviculture guidelines and aboveground biomass on woody species regeneration

We found a total of 42 native woody species and 1,638 individuals regenerating in the plantation understory (total sampled area of 0.23 ha, combining all plots and treatments). Seventy-four percent of regenerating

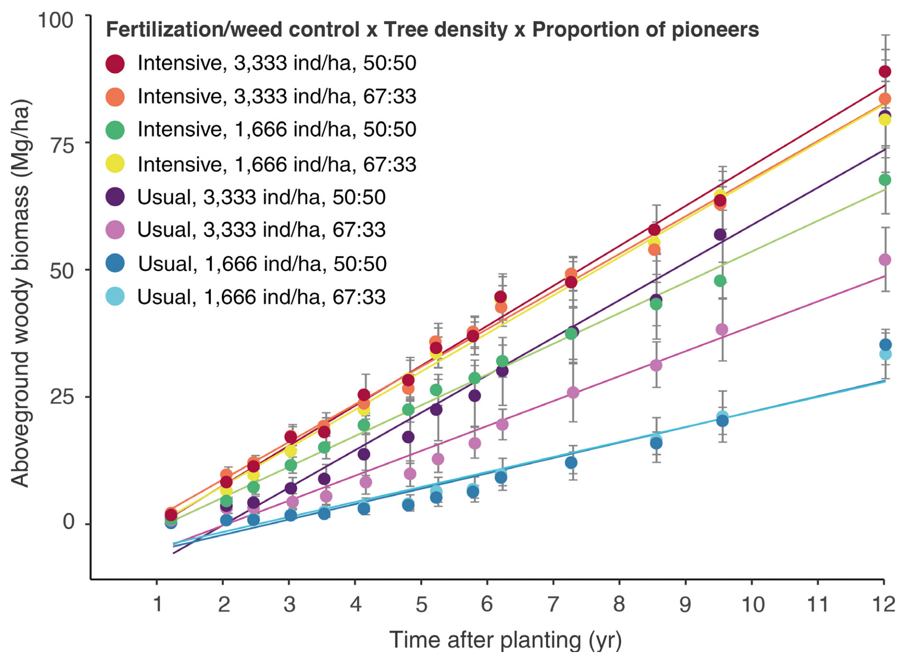

FIG. 2. Aboveground woody biomass accumulation in an experimental tree plantation managed under contrasted silvicultural intensity treatments in the Atlantic Forest of Brazil. Usual and intensive refer to the intensity of the fertilization and wood control, the numbers of individuals (ind.) per hectare refer to the tree density of the planting, 50:50 and 67:33 refer to the proportion of pioneers species in the planting (50% and 67%, respectively).

TABLE 1. Effects of silviculture intensity treatments, age, and their interaction in the accumulation of aboveground woody biomass in an experimental tree plantation established in the Atlantic Forest of Brazil.

	Results of log-likelihood ratio test	
Factors	$\chi^2_{(\text{df}=1)}$	*P*
Fertilization/weed control	15.73	<0.0001
Age	1,007.16	<0.0001
Fertilization/weed control × Age	13.78	<0.0001
Tree density	0.64	0.424
Age	833.75	<0.0001
Tree density × Age	6.24	0.90
Proportion of pioneers	0.50	0.479
Age	690.95	<0.0001
Proportion of pioneers × Age	0.03	0.855

Notes: Age effects consider 14 forest inventories performed from the first to the 12th year after planting. Mixed-effects models were adjusted as follows: lmer(log transformed biomass ~ Treatment + Age + Treatment × Age + [Age|Plot]).

individuals were of *Senegalia polyphylla* (DC.) Britton & Rose, a planted legume tree (Appendix S1). Three-quarters of all regenerating species were not planted, and 90% of the colonizing species and 95% of the colonizing individuals were dispersed by animals (Appendix S1). The regeneration of both planted and colonizing species was highly influenced by silvicultural intensity treatments (Table 2). Usual fertilization/weed control decreased the abundance and richness of both planted and colonizing species, whereas the density of planted trees and proportion of pioneers had contrasting effects depending on the origin of species: the regeneration of planted species benefited from reduced density of trees and higher proportion of pioneers, while the regeneration of colonizing species was negatively affected by them (Table 2). Although the regeneration of planted species was not significantly affected by AGB ($P > 0.10$), higher AGB greatly favored the regeneration of colonizing species ($P < 0.001$; Fig. 4).

Ecological processes driving woody species regeneration in the understory

The regeneration of colonizing trees (both abundance and species richness) was favored by increasing basal area of neighboring planted trees and higher iPAR throughout the year (dry and wet seasons); but, contrary to our expectation, it was not negatively affected by grass cover (Fig. 5). Grass cover was not negatively affected by iPAR, but was affected by litter biomass in the dry season (Fig. 5). Litter biomass fostered the number of regenerating individuals of colonizing species in the dry season (Fig. 5).

DISCUSSION

Intensive silviculture demonstrated a remarkable potential to enhance carbon accumulation in restoration plantations by increasing up to three times the AGB of tree stands. Contrary to our hypothesis, we did not find a trade-off between carbon accumulation and native woody species recovery, since intensive silviculture enhanced the regeneration of both planted and colonizing woody species in the plantation understory, most of the latter being dispersed by animals. We therefore report a case of positive correlation between carbon stocking and woody species regeneration in the restoration of the Atlantic Forest.

How does silviculture affect biomass accumulation in a tropical restoration planting?

Intensive fertilization and weed control turned out to be the most effective silvicultural treatment to maximize biomass accumulation. As expected, increased nutrient availability from higher fertilization inputs and reduced competition with invasive aggressive C_4 grasses accelerated tree growth at our nutrient-poor study site. The benefits of intensive fertilization and weed control described here corroborate those observed in the same experiment three (Campoe et al. 2010) and six (Ferez et al. 2015) years after planting, thus evidencing the persistent positive impacts of this treatment for biomass accumulation in the first decade of plantation. Enhanced biomass accumulation under intensive fertilization and weed control likely resulted from higher primary productivity, promoted by the release of nutrient limitation and reduced competition for water on photosynthesis, and increased leaf area index and light use efficiency (Campoe et al. 2014). The benefits of intensive fertilization and weed control for biomass accumulation was mainly observed at low tree density, as higher competition probably constrained tree responses in high density plantations (Dobbertin 2005).

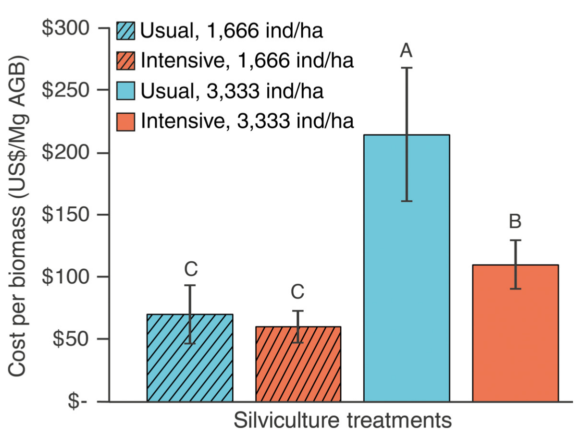

FIG. 3. Cost per aboveground biomass (AGB) accumulated in an experimental tree plantation managed under usual and intensive weeding and fertilization and planted with different seedling densities in the Atlantic Forest of Brazil. Different letters over the bars represent statistically different means (Tukey test, $P < 0.05$) and error bars represent the standard deviation.

Tree density did not affect AGB accumulation in the first 3 yr after planting (Campoe et al. 2010), but high density of trees positively affected it in the subsequent stages of plantation development. The lower density level tested here represented the typical density (1,000–1,700 trees/ha) employed in restoration plantations in the Atlantic Forest (Rodrigues et al. 2011), Costa Rica (Zahawi et al. 2015), and Panamá (Potvin et al. 2011), whereas restoration plantations with higher tree density (~3,000 trees/ha) have been used in Australia (Kanowski and Catterall 2010), and Thailand (Elliott et al. 2003). As discussed above, plantations with higher density of trees accumulate more biomass per area than lower density plantations under usual fertilization and weed control. The presence of more trees per area may have compensated the reduced individual growth caused by reduced nutrient availability and competition with grasses in the usual fertilization/weed control plots. Planting higher density of trees can thus be an alternative when the use of high fertilization inputs and glyphosate spraying is unpractical or avoided by practitioners, like in the restoration of riparian forests or in projects located within Protected Areas or catchments supplying drinking water to people. However, such strategy would increase restoration costs considerably (57–65%; Appendix S1) and could be difficultly used at large scale. Higher tree density may also reduce the growth of individual trees and compromise their seed production, a

TABLE 2. Effects of silvicultural intensity on the regeneration of planted and colonizing tree species in an experimental tree plantation established in the Atlantic Forest of Brazil.

	No. individuals			No. species		
Species origin/Treatment	Estimate	Z	P	Estimate	Z	P
A) Planted species						
Proportion of pioneers (67:33)	0.37	2.16	0.03	0.19	1.06	0.29
Fertilization/weed control (intensive)	0.48	2.82	0.0047	0.44	2.45	0.014
Tree density (3,333 individuals/ha)	−1.32	−6.40	<0.0001	−1.18	−5.67	<0.0001
B) Colonizing species						
Proportion of pioneers (67:33)	−0.07	−1.27	0.20	−0.28	−3.17	0.0015
Fertilization/weed control (intensive)	0.86	14.84	<0.0001	0.59	6.44	<0.0001
Tree density (3,333 individuals/ha)	0.82	14.26	<0.0001	0.41	4.56	<0.0001

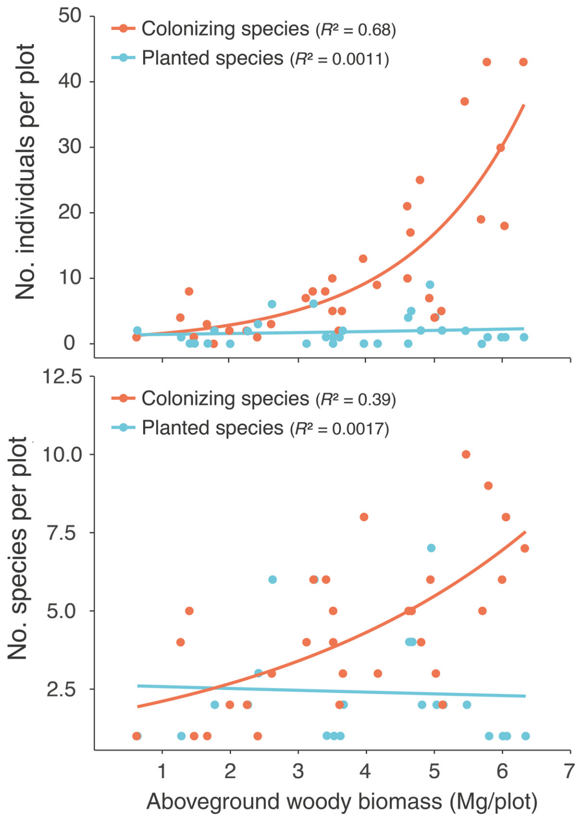

FIG. 4. Relationship between aboveground biomass (AGB) and the abundance and richness of planted and colonizing species at the plot level (72 m^2 sampled per plot) in an experimental tree plantation established in the Atlantic Forest of Brazil. R^2 values represent the pseudo-R^2 of McFadden. Association between aboveground biomass and the abundance and richness of colonizing species are expressed by the following equations: $\log_{(density)} = -0.17441 + \Sigma AGB \times 5.88^{-4}$ and $\log_{(richness)} = 0.47461 + \Sigma AGB \times 2.32^{-4}$.

potential explanation for the negative association between higher planting density and recruitment of planted species, in contrast with the improved recruitment of colonizing species in denser, high AGB plantations. Moreover, adopting an intensive management and planting more trees per area may accelerate biomass accumulation in the first years of plantations, but may not result in higher AGB stocks in the long term, as evidenced by the higher biomass increment overtime of less intensive silviculture treatments.

The absence of a significant effect of the proportion of pioneers on AGB stocking suggests that the proportion of 50% of pioneers found in our low pioneer level was sufficient to reach early canopy closure and high initial biomass accumulation (Shimamoto et al. 2014). As non-pioneer species have denser wood, can achieve larger size, and live longer, using 50% pioneers is preferable to obtain a more complex forest structure and higher biomass stocks in the long term. Pioneer species commonly present features of fast resource acquisition strategy (Reich and Cornelissen 2014), such as low wood density, high specific leaf area, and low ability to tolerate competition (Kunstler et al. 2015). Consequently, higher proportion of pioneers in restored forests may lead to an increase in competition intensity among fast-growing tree species, and to a saturation of the pioneer proportion effect on AGB at the stand level. We note, however, that our result may partly be a consequence of limitations in the classification of species, as several species demonstrated a field-growth behavior different from what was expected when selecting species for the experiment (Campoe et al. 2010). Such divergences in the expected and realized performances of pioneer species are common in restoration plantations in the region, as species performance is highly influenced by genetics, soil and climate conditions, plantation management, and competition with neighboring trees.

How does silviculture affect woody species regeneration in a tropical restoration planting?

Intensive silviculture positively influenced the natural regeneration of woody species in the plantation understory, especially of colonizing species (Fig. 4). On the other hand, planted species had a poor regeneration, with the exception of the hyperabundant legume tree *S. polyphylla* (Fig. 4; Appendix S1). We speculate that this observation results from a strong light limitation in the understory for seed germination and seedling establishment of pioneer species. This is in line with our finding that the vast majority of regenerating species were dispersed by animals. Animal seed dispersal has indeed for long been associated to shade-tolerant species (Foster and Janson 1985). The time since plantation was likely insufficient (12 yr) in this study for the planted shade-tolerant species to reach maturity, and produce seeds, which led to a disproportional amount of colonizing species regenerating in the understory. The high diversity of colonizing species regenerating in the restoration plantation was an unexpected positive result, as the plantation was established in a landscape with very few surrounding native forest remnants. The establishment of commercial woodlots (*Eucalyptus* and *Pinus* genus) across the landscape and restoration plantations with native species in riparian buffers (Fig. 1) may have increased the flow of seeds and dispersing fauna (Metzger and Brancalion 2013), thus contributing to the progressive recolonization of the plantation understory by native trees.

Remarkably, the vast majority of colonizing individuals and species were dispersed by animals, as also observed in other restoration plantations of the region (Schweizer et al. 2015, Suganuma and Durigan 2015, Viani et al. 2015, César et al. 2018). Most of the regenerating tree species were medium-seeded, bird-dispersed species, a common feature in a degraded tropical habitat context (Lindell et al. 2013, Reid et al. 2015). However, two species had relatively large seeds dispersed by birds

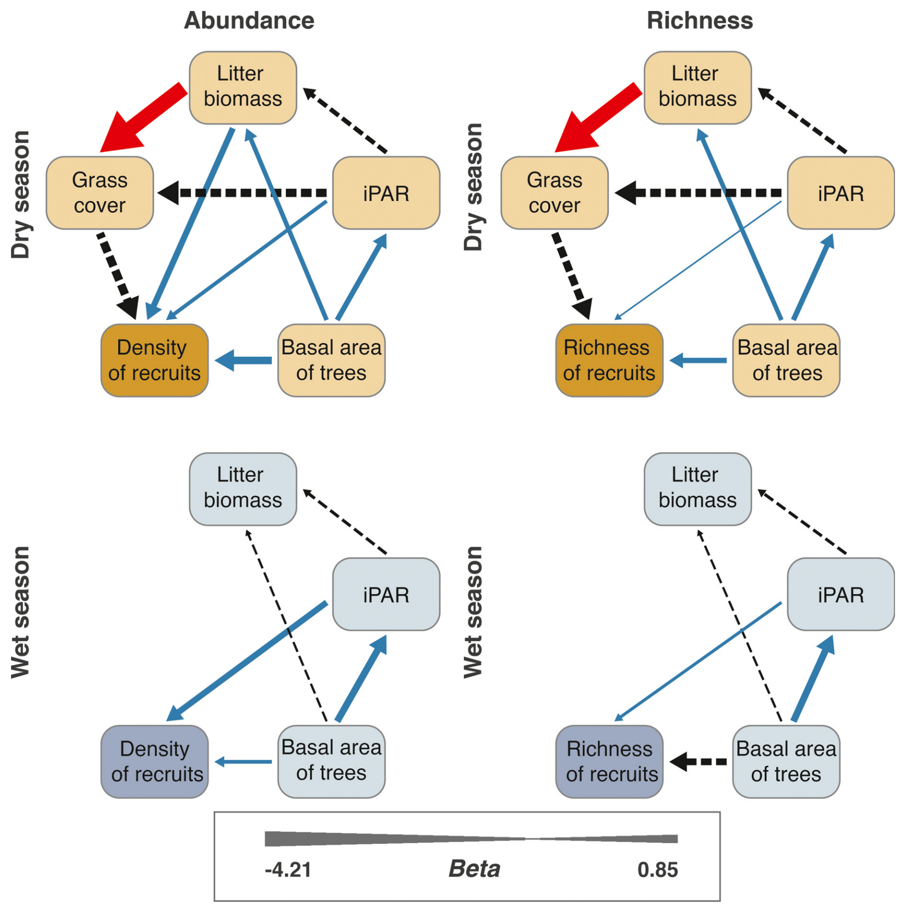

Fig. 5. Structural equation models showing the relations among different plantation features and the density and richness of colonizing tree species in the dry and in the wet seasons in an experimental tree plantation established in the Atlantic Forest of Brazil. Red solid line arrows represent significant negative associations, blue solid line arrows significant positive associations, and black dotted arrow nonsignificant associations. The thickness of arrows represents the value of the path coefficient (Beta) that quantifies the strength of intervariable dependencies. Photosynthetically active radiation intercepted by the canopy is abbreviated iPAR.

(*Endlicheria paniculata* (Spreng.) J.F.Macbr., 12.5 mm seed diameter; *Copaifera langsdorffii* Desf., 11.0 mm seed diameter) and two were predominantly dispersed by mammals (*Syagrus romanzoffiana* (Cham.) Glassman, and *Genipa americana* L.). This highlights the value of restoration plantations for the conservation of large-seeded tropical trees that usually have reduced dispersal across degraded landscapes (Reid et al. 2015, Brancalion et al. 2018).

The benefits of intensive silviculture and the positive association between biomass and biodiversity recovery were highlighted by the structural equation modeling analysis, which allowed us to untangle the ecological processes through which biomass affected the regeneration of colonizing species (Fig. 5). The basal area of neighboring planted trees and the iPAR, which was positively influenced by tree basal area, were the most influencing factors in enhancing the regeneration of colonizing trees. Contrary to our expectations, both tree basal area and iPAR were not inversely associated to the presence of *U. decumbens*, which did not exert a negative influence on natural regeneration. The lack of grass influence on regeneration may be related to a limitation of the method used to assess ground cover by grasses, as the use of small plots (0.5 × 0.5 m) did not allow for the evaluation of grass cover as a continuous variable, which may have limited the detection of statistical significance. In parallel, the lack of influence of tree basal area and iPAR on grass incidence may be associated to edge effects, since the plantation experiment was established in a narrow vegetation strip along a water reservoir (width ranging from 40 to 80 m), which followed Brazilian guidelines to restore riparian buffers (Fig. 1; Brancalion et al. 2016*a*). Consequently, it is likely that grasses benefited in all the experiment plots from lateral light incidence, a common feature related to edge effect in fragmented forests (Xiong and Nilsson 1999). Lateral light incidence is not captured by iPAR measurements, which are related to the amount of light intercepted vertically by the canopy. In this condition, litter accumulation on the ground in the dry season, when several trees shed their leaves in this tropical region, was the major driver of grass suppression. The important role of leaf litter in suppressing grass germination and establishment and influencing tree species succession has been long known in natural forests (Murcia 1995) and is shown here to be significant in patched restoration plantations.

Biomass–regeneration positive association: management implications

The positive association between biomass stocks and the diversity and abundance of colonizing species may be associated to both the attractiveness of the vegetation structure to seed dispersing fauna and the availability of safe sites for seedling establishment (Reid and Holl 2013, Bertacchi et al. 2016, Wheeler et al. 2016). Complex forest structures, with reduced grass cover and abundant regeneration in the understory, are known to attract more birds to restoration sites (Wunderle 1997, Munro et al. 2011, Reid et al. 2012, McAlpine et al. 2016). Intensive silvicultural treatments appeared to create a virtuous cycle for understory regeneration: a more developed forest structure may attract more seed dispersing fauna and enhance seed arrival, which will find appropriate microsites for seedling establishment (i.e., a more shaded understory and lower competition with invasive grasses). Such favorable regeneration conditions would allow the establishment of a more abundant and species-rich understory community of animal-dispersed woody plants, which in turn would attract more dispersers and more seeds to restoration sites. Importantly, the cost effectiveness of intensive silviculture was shown to be similar to the cost effectiveness of traditional silviculture (Fig. 3), while reaching higher carbon and biodiversity benefits. Investing in intensive silviculture may thus be a smart choice in both financial and ecological terms. The positive results of intensive silviculture on carbon accumulation and biodiversity benefits of restoration plantations rise questions related to the isolated significance of the treatments. Is weed control more important than fertilization? Therefore, we suggest the development of new experimental designs isolating the effects of fertilization and weed control to address this question.

Restoration objectives go far beyond the establishment of a successful tree plantation with high biomass stocks and usually aim at increasing the ecological integrity and long-term sustainability of the ecosystem (Suding et al. 2015, McDonald et al. 2016). In line with the main finding of our study, a positive relationship between biomass and tree diversity has been previously reported in both natural (Liang et al. 2016) and experimental contexts (Potvin and Gotelli 2008, Huang et al. 2018). These results have led to strong calls for multispecies afforestation strategies in order to mitigating climate change while sustaining forest productivity (Hulvey et al. 2013, Huang et al. 2018). In addition, tropical forest restoration has for long promoted the plantation of native tree species mixtures as a way to promote biodiversity conservation (Rodrigues et al. 2011, Shoo et al. 2016, Lamb 2018), with the expectation that a higher tree diversity will attract more dispersers and create better microsites for colonizing species. Here, we demonstrated that the increase of biomass accumulation mediated by intensive silviculture plays in turn a crucial role for biodiversity recovery in restored forests. Optimal fertilization and weed control, rather than high density and functional diversity of the planting, were shown to significantly enhance biomass accumulation and biodiversity recovery in the context of our study. Fostering the establishment and productivity of restoration tree plantations can in some cases be a win-win strategy for cost-efficient climate mitigation and biodiversity conservation in human-modified tropical landscapes.

Acknowledgments

We thank the National Council for Scientific and Technological Development of Brazil (CNPq; grant #304817/2015-5) and the São Paulo Research Foundation (FAPESP; grant # 2012/05814-3, #2013/50718-5) for financial support, and Grupo Florestal Monte Olimpo for field work support. The implementation of the experiment was supported by Petrobras Company, Forestry Science and Research Institute (IPEF), and the Anhembi Experimental Station of Forest Sciences of the University of São Paulo. We acknowledge support from the IN-SYLVA French network.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1847/full

Data Availability

Data are available at Zenodo (https://doi.org/10.5281/zenodo.2121072)