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What deters plant colonization in a tropical pine plantation?

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Abstract: Pine plantations in the tropics are often employed to recondition eroded slopes from mudslides, as the *Pinus caribaea* plantation that shields the Universidad Simón Bolívar campus in Caracas (Venezuela). However, mismanagement of this plantation has led to its rapid degradation. The best option to maintain the protective service is to restore the plantation and direct its successional trajectory towards the neighbouring montane forest. Through experimental manipulation, we aimed to determine which factors block secondary succession and to investigate their effects. Within the experimental constraints imposed by the plantation small area, we analysed the effects of light and fertility limitation, litter accumulation and access to seed on plantation restoration. Light availability was manipulated by clearing and thinning three 800 m^2 main plots. Fertilization and litter removal was applied to sub-plots within the light plots. Soils were analysed, microclimate was monitored and, for four years, stem density, species richness and basal area were tallied. Our results showed that light accessibility was the main factor deterring the successional trajectory of the plots, with varying grades of interaction with the sub-treatments. By the end of the fourth year, the cleared plot showed the largest responses in all traits (triplicating stem density and basal area and >20 times higher species richness). The main colonizers were *Croton megalodendron*, *Ocotea fendleri*, and *Clusia* spp. all dominant trees in the nearby native forest. We concluded that the results of this pioneer study, showed that small clearings, repeated in 3-4 year cycles are appropriate for similar restoration schemes. This procedure would create a mosaic of vegetation patches at different successional stages while protecting the slopes from erosion and increasing local biodiversity. Rev. Biol. Trop. 64 (2): 461-471. Epub 2016 June 01.

Key words: light limitation, passive restoration, pine needle litter, *Pinus caribaea,* Venezuela.

Since colonial times, Neotropical montane forests have been severely degraded by deforestation for firewood, charcoal manufacture and cultivation. Afterwards, recurrent fires blocked secondary succession and the slopes became subjected to erosion and mudslides. In some instances, protective reforestation of these areas was attempted, mostly with *Pinus* species (FAO, 2010) as they establish rapidly, grow fast and propagate easily. However, tropical pine species are short-lived and their plantations are frequently mismanaged leading to degradation and fire hazards. Consequently, to continue providing the required protection services, they must be restored. This approach has been attempted in the tropics and its success in promoting secondary succession is highly site specific (Ashton et al., 2014). It is subjected to local climate and soils (Fimbel & Fimbel, 1996), plantation age (Lugo, 1992), proximity to seed sources and their dispersers (Keenan, Woldring, Irvine, & Jensen, 1997; Zanne & Chapman, 2001) and management systems (Wadsworth, 2008). Furthermore, restoration in pine plantations is hindered by allelopathic metabolites from roots or litter that interfere with colonization and growth of successional species (Fernández et al., 2006; Nissanka, Mohotti, & Wijetunga, 2005; Guerrero & Bustamante, 2007).

The pine plantation of the Universidad Simón Bolívar (USB) Caracas (Venezuela) shields the campus from mudslides. Established ~40 years ago, the plantation also delivers recreational services, landscape amenity and educational and research opportunities. Since the plantation was providing excellent services it was never thinned as reforestation practice recommends. This management decision disregarded the limitations of tropical pines and that restoration was required to preserve their ecological value. The lack of clear ecological long-term goals has led to gradual plantation decline which offered us the opportunity to set a passive restoration research.

Our objective was to assess experimentally the effects of factors that prevent restoration and to discuss some management options which could accelerate and guide a desirable successional trajectory to resemble the adjacent montane forest. We evaluated the effects of pine clearing and thinning, combined with fertilization and litter removal, on the recruitment and growth of native species. To our knowledge, this is the first study of this type attempted in the Neotropical montane forest biome and its results may assist in the restoration of comparable pine plantations.

MATERIALS AND METHODS

Study site and experimental design: The plantation extends over 48 ha (10°24' N - 66°53' W; 1 100-1 450 masl; Fig. 1A.) on slopes previously covered with secondary scrub and savanna which had encroached after deforestation of the montane forest. Reforestation was done mostly with Caribbean pine (*Pinus caribaea* Mortelet) (AGROFORCA, 1990). The study site is on 15-30 % slopes, over quarzitic schists, capped by shallow, acidic and unfertile soils. The climate is temperate with most rainfall from May to December. On its Southern edge, 20-30 m separate the plantation from a 103 ha fragment of montane forest (Baruch & Nozawa, 2014; Fig. 1A.) which is a potential seed source for plantation recruitment. Currently, formal status of the whole area is catalogued as "a conserved or protected zone". Its use is restricted to a few sport activities along trails and its management includes relative safeguard from fire and human encroachment.

The small area and the protective role of the USB plantation constrained the experimental design which impeded replication. We selected one 2 400 m^2 (60 x 40 m) area and divided it into three 800 m^2 (20 x 40 m) main plots. Light availability treatments were imposed by manipulating pine density and were randomly assigned to plots by: (1) clearing all pines (L100); (2) thinning approximately half of the pines (L50); and (3) leaving the control plot intact (L0) (Fig. 1B). Timber felling and log disposal might have damaged some undergrowth plants and pine regeneration was nil. Within each main plot, twelve 15 m^2 (3 x 5 m) sub-plots were established and delimited. Four sub-treatments were randomly assigned to three replicated sub-plots: (1) untreated controls (sub-treatment C); (2) raking of the litter (sub-treatment A); (3) litter removal by fire (sub-treatment F); and (4) fertilizer application with granulated NPK (15-15-15) at 200 kg/ha (sub-treatment N) (Fig. 1B). The remaining of each main plot area (620 m^2) was divided into four quadrants of 155 m^2 for additional vegetation sampling (Fig. 1B). Vegetation was left to regenerate either by recruitment or by continued growth (or death) of that already present (Fig. 1C).

Climate, microclimate and soils: A nearby climatological station provided long term (1972-1992) rainfall data. Throughout the study, air temperature, relative humidity and rainfall were recorded inside and outside the plantation with HoBo loggers (model H08-032-08, ONSET, Bourne, MA, USA) and standard pluviometers. Canopy cover and leaf area index (LAI) were measured with hemispheric photography (Nikon, Cool-Pix 4500 and Fisheye Converter, FC-E8, 0.21x) taken from the centre

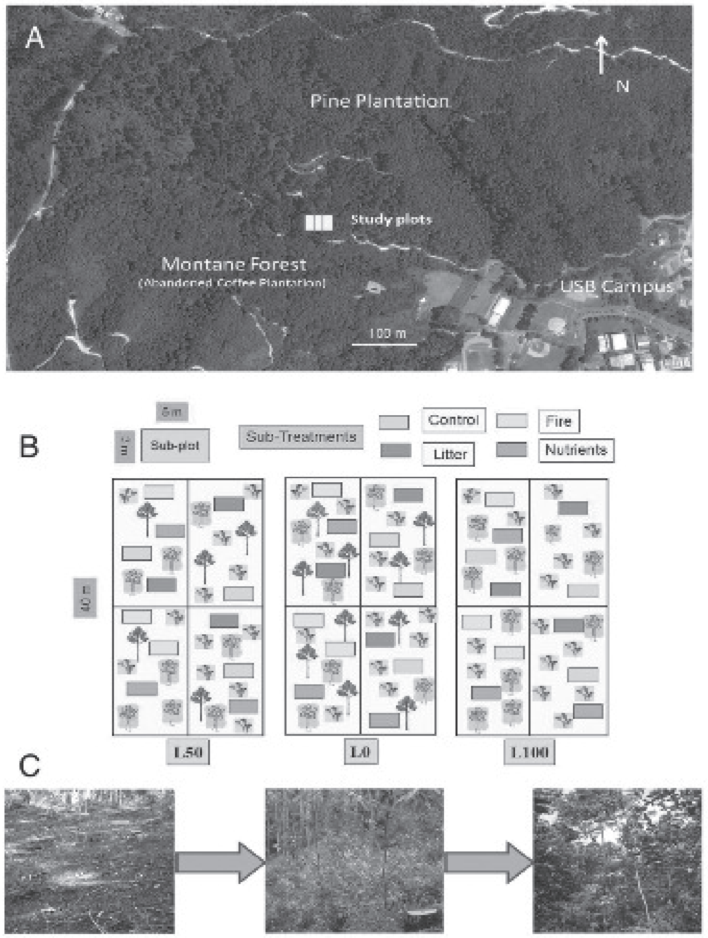

Fig. 1. (A) Pine plantation and adjacent montane forest showing site of experimental plots. Approximate scale 1:10.000. (B) Scheme of the experimental design of main plots, sub-treatment plots and quadrants. (C) Vistas of cleared plot (L100) from 2008 (left), 2009 (centre) and 2012 (right).

of four quadrants within intact plots. Images were analysed with HemiView software (Delta-T Devices Ltd., Houston, TX, USA).

Nine months after imposing the sub-treatments, one soil sample was collected from the centre of each of the 36 sub-plots. After air-drying, texture was obtained by the Bouyoucos technique, available phosphorus was analysed with the molybdic-blue method (Murphy & Riley, 1963), whereas potassium and calcium were determined by flame spectrophotometry. Total nitrogen was analysed after Kjehdal digestion. Cation exchange capacity (CEC) and exchangeable aluminium content were analysed by extracting with NH_4Cl, followed by spectrophotometry (Sparks et al., 1996). Organic matter (Walkley & Black's method; Jackson, 1982) and pH (1: 2.5 in water) were also measured. A synthetic integrated fertility index (FI) was calculated for each plot as the sum of the relative values (with respect to their maximum) of N, P and CEC (maximum FI = 300). Soil apparent bulk density was tested on four samples per plot, and soil litter was collected with a circular sampler from 12 plot locations, oven-dried and weighed. Throughout the study, soil water content (SWC), at 5 cm -10 cm depth, was analysed gravimetrically, on six samples per main plot.

Vegetation sampling and monitoring: In all sub-plots and quadrants, tree and shrub individuals with diameter at breast height (DBH) > 1 cm were identified, tallied and labelled with metallic tags. DBH at ~ 1.3 m above soil was obtained by averaging two perpendicular diameters and converted to basal area (BA). Stem diameter of shorter individuals was taken below the first branching. The presence and abundance of herbaceous vegetation and woody saplings < 1 cm DBH were visually estimated. Botanical samples were collected, photographed, processed and identified as in Hokche, Berry, & Huber (2008). Vouchers are deposited in the USB herbarium. When identification was impossible, individuals were assigned to family or morphotype. Surveys were performed at the end of the rainy season (October-January) from 2008 to 2012. Due to logistical issues, the last census could not be completed.

Within the limitations of available experimental area stated above, we considered the three main light plots as blocks for treatment comparisons. Differences in soil properties among treatments were tested with a two-way ANOVA (SYSTAT, 2002). To avoid interference caused by remaining pre-treatment vegetation within plots, we analysed only yearly vegetation traits changes after the initial 2008 survey. To ease interpretation of differences between sub-treatments, only differences between initial and final results were analysed. Due to lack of multivariate normality in vegetation traits results, one and two-factor PerMANOVA tests were applied to differences between plots, treatments and years (PC-Ord; McCune & Mefford, 2011). To better represent multivariate data, we drew polygons of ordered plots within the vegetation trait space obtained by principal component analysis (PCA) and indicated by successional vectors (PC-Ord; McCune & Mefford, 2011).

RESULTS

Climate, microclimate and soils: Climate is relatively mild (20.2 °C mean temperature) and long term mean rainfall is 1 006.1 mm but with large inter-annual variation. Through the study, year 2009 was relatively dry (673.8 mm), 2010 and 2011 were wet (1 546.5 and 1 607. 8 mm, respectively), whereas 2012 has close to average rainfall (1 113.9 mm). Pine canopy retained 24.1 ± 6.3 % of rainfall. Before clearing and thinning, the plots did not differ in canopy cover or LAI (Table 1) which buffered the microclimate. In consequence, maximum mean and absolute temperatures as well as the temperature range were the highest in the cleared plot, whereas air relative humidity was always the lowest (Table 1).

Soils were unfertile and acidic sandy loams (Table 2). Needle litter accumulated up to 30 cm in depth and averaged 2.01 ± 0.43 kg/m^2, whereas soil bulk density was 1.10 ± 0.15 g/cm^3. Soils from the sub-treatments differed significantly in N, C, and K concentration, CEC and in FI (Table 3). Those from the burned needle sub-treatments (F) were expected to show the lowest nutrient content and FI, whereas fertilization sub-treatments (N) were expected to show the highest values. However, neither was supported by the results. SWC mirrored canopy interception, seasonality and yearly rainfall; it was always the highest in the cleared plot. During the dry season of the “dry” year (2009), the cleared plot averaged 35 % more SWC than in the intact plot.

Vegetation traits: Vegetation changes were the fastest in the cleared plot where, after the first rainy season, tall and dense graminoids colonized and overtopped recruited seedlings. By the last survey, graminoids had almost disappeared and 47 woody species from 21 families were tallied (Fig 1C). Owing to their high stem density and BA, *Croton megalodendron* (Euphorbiaceae), *Ocotea fendleri* (Lauraceae), *Clusia* spp. (Clusiaceae), *Roupala montana* (Proteaceae) and *Myrcia fallax* (Myrtaceae) were the most important trees.

TABLE 1
Microclimate in the experimental plots

	PLOT L100	PLOT L0	PLOT L50
a-Temperature (°C)			
Mean Maximum	26.6 (3.2)	24.9 (2.3)	24.5 (2.1)
Mean Minimum	16.6 (1.0)	16.6 (1.0)	16.8 (0.9)
Range (Max - Min)	9.9	8.3	7.7
Max absolute	36.3	30.0	30.7
Min absolute	13.6	13.9	13.8
Relative Humidity (%)			
Mean minimum	69.6 (15.1)	73.0 (13.6)	73.7 (14.2)
Min absolute	26.5	36.0	34.0
b-Radiation environment			
Canopy Cover (%)	74.0 (2.4)[a]	67.7 (3.0)[a]	77.1 (1.9)[a]
LAI	2.0 (0.3)[a]	1.9 (0.1)[a]	2.6 (0.7)[a]

L100 (cleared); L50 (thinned); L0 (control) a- Mean, range and absolute air temperature and relative humidity as monitored during 160 weeks. b- Radiation environment: Canopy cover and leaf area index (LAI) before clearing and thinning. Standard deviations in parentheses. Values followed by the same superscript letter were not statistically different at $p<0.05$.

TABLE 2
Mean and standard deviation of soil physicochemical parameters* of sub- treatments within main light plots

PLOT	Sub-Treat	Sand	pH	N	CEC	Ca	K	P	OM	FI
L100	Control	47.88	4.50	0.11	8.31	0.40	0.03	4.33	4.57	151.18
		1.92	0.10	0.02	2.94	0.07	0.01	0.58	0.39	10.84
L100	Fire	49.30	4.63	0.15	7.90	0.40	0.04	5.67	4.34	184.38
		2.66	0.12	0.04	2.52	0.03	0.02	0.58	1.88	31.68
L100	Raking	48.13	4.53	0.10	10.27	0.39	0.05	4.00	3.63	149.54
		4.31	0.21	0.01	3.05	0.10	0.01	0.00	0.27	16.69
L100	Fertilizer	45.25	4.57	0.10	6.95	0.34	0.03	4.67	3.65	142.80
		0.76	0.25	0.01	1.80	0.02	0.01	0.58	0.67	6.28
L50	Control	44.05	4.37	0.15	15.91	0.44	0.07	4.33	4.95	206.36
		4.69	0.12	0.02	3.49	0.10	0.02	0.58	0.57	22.92
L50	Fire	47.75	4.70	0.12	11.04	0.54	0.04	4.33	3.85	169.93
		3.56	0.44	0.01	2.04	0.36	0.01	0.58	0.44	10.97
L50	Raking	44.54	4.57	0.12	11.32	0.44	0.06	4.33	3.73	169.43
		1.31	0.12	0.01	3.10	0.11	0.01	0.58	0.33	13.75
L50	Fertilizer	45.04	4.53	0.13	15.45	0.52	0.06	5.33	4.88	204.17
		3.12	0.12	0.01	5.52	0.12	0.03	1.53	0.89	15.72
L0	Control	49.26	4.60	0.16	14.83	0.58	0.08	6.33	5.48	230.79
		3.00	0.17	0.02	1.37	0.20	0.02	2.31	1.00	35.21
L0	Fire	44.32	4.63	0.14	7.56	0.39	0.04	4.00	4.39	156.82
		2.20	0.06	0.03	3.65	0.04	0.02	0.00	0.73	10.23
L0	Raking	47.25	4.67	0.13	5.78	0.37	0.04	6.67	4.00	172.34
		5.67	0.12	0.02	2.22	0.15	0.02	2.52	0.59	14.37
L0	Fertilizer	48.25	4.60	0.13	8.22	0.46	0.04	5.00	4.06	167.41
		4.36	0.17	0.03	5.28	0.12	0.03	1.73	0.81	28.47

*Total N (%), available P (ppm), Organic matter (OM, %), Sand (%). Fertility index (FI; max = 300). Cation Exchange Capacity (CEC), Ca, K (cmol/kg).

TABLE 3
Two-way ANOVA of selected soil traits

Variable	Source	F-ratio	P
NITROGEN	PLOT	$F_{(2,24)} = 3.67$	0.040
	TREATMENT	$F_{(3,24)} = 3.40$	0.340
	INTERACTION	$F_{(6,24)} = 1.77$	0.147
CARBON	PLOT	$F_{(2,24)} = 0.87$	0.420
	TREATMENT	$F_{(3,24)} = 3.43$	0.033
	INTERACTION	$F_{(6,24)} = 0.77$	0.594
CEC	PLOT	$F_{(2,24)} = 8.18$	0.002
	TREATMENT	$F_{(3,24)} = 2.97$	0.050
	INTERACTION	$F_{(6,24)} = 1.83$	0.134
MAGNESIUM	PLOT	$F_{(2,24)} = 4.84$	0.017
	TREATMENT	$F_{(3,24)} = 2.11$	0.125
	INTERACTION	$F_{(6,24)} = 1.79$	0.144
POTASSIUM	PLOT	$F_{(2,24)} = 3.30$	0.050
	TREATMENT	$F_{(3,24)} = 2.66$	0.071
	INTERACTION	$F_{(6,24)} = 2.15$	0.084
FERTILITY INDEX	PLOT	$F_{(2,24)} = 7.76$	0.003
	TREATMENT	$F_{(3,24)} = 4.45$	0.013
	INTERACTION	$F_{(6,24)} = 4.68$	0.003

Only variables with significant effects between main plots, sub-treatments and/or interactions are shown.

TABLE 4
Two-way PerMANOVA of differences between sub-treatments within the main plots

TRAIT	Factor	F	P
Stem Density	Plot	$F_{(2,35)} = 19.02$	0.0002
	Sub-treatment	$F_{(2,35\ )} = 2.31$	0.1180
	Interaction	$F_{(4,35)} = 2.13$	0.0092
Species Richness	Plot	$F_{(2,35)} = 10.57$	0.0002
	Sub-treatment	$F_{(2,35)} = 1.05$	0.3660
	Interaction	$F_{(4,35)} = 1.03$	0.4280
Basal Area	Plot	$F_{(2,35)} = 0.93$	0.4000
	Sub-treatment	$F_{(2,35)} = 0.27$	0.7580
	Interaction	$F_{(4,35)} = 1.34$	0.2760

Clearing increased stem density and species richness but BA was unaffected (Fig. 2 and Table 4). The small area (15 m^2) of the sub-treatment plots was probably the main cause for the large differences among replicates (Fig. 2). The results from the much larger quadrants stress the positive effect of light availability on stem density and BA but not on species richness (Fig. 3 and Table 5). Also, year to year differences were significant in stem density and BA (Fig. 3 and Table 5). The large polygon area in the PCA ordination diagram, and the length of the successional vector (Fig. 4), confirms the pronounced multitrait changes promoted by increased light.

DISCUSSION

The initial densely sown pines, and subsequent absence of thinning, probably hindered understory recruitment by the combined effects of: (1) decreased light availability;

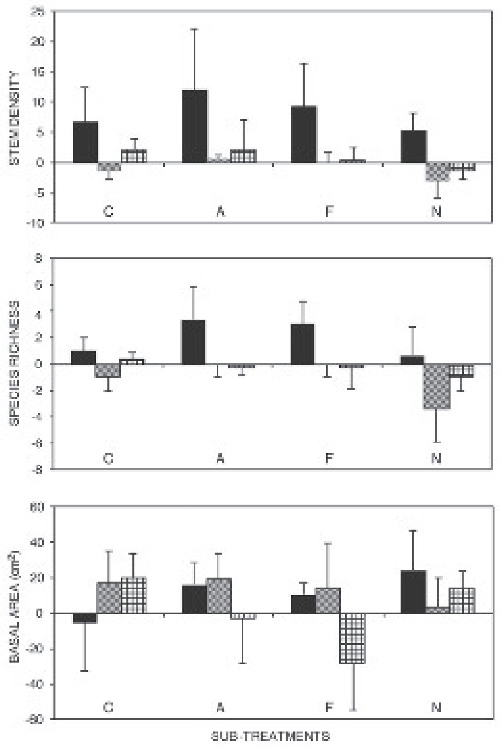

Fig. 2. Differences between the final (2011) and initial (2008) surveys values of stem density, species richness and basal area of the sub-plot treatments. Filled bar = cleared plot (L100); Grey bar = thinned plot (L50); Stripped bar = control plot (L0). Sub-treatments: C = Control; A = Litter removal by raking; F = Litter removal by fire; N = Nutrient addition.

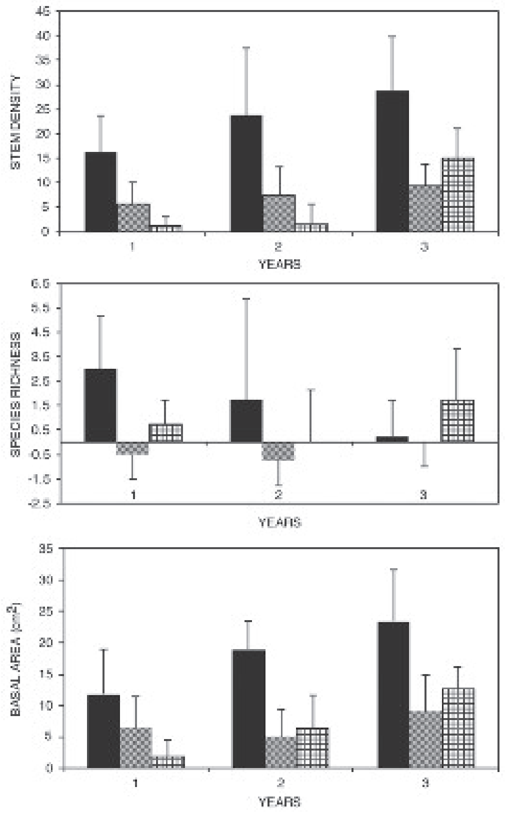

Fig. 3. Stem density, species richness and basal area of the quadrants from the main light plots through the study. (Filled bar = cleared plot (L100); Grey bar = thinned plot (L50); Stripped bar = control plot (L0).

TABLE 5
Two-way PerMANOVA analysis of differences between main light plots, sampling years and their interaction

TRAIT	Factor	F	P
Stem Density	Plot	$F_{(2,35)} = 12.31$	< 0.0001
	Year	$F_{(2,35)} = 4.53$	0.0128
	Interaction	$F_{(4,35)} = 0.67$	0.6290
Species Richness	Plot	$F_{(2,35)} = 3.15$	0.0570
	Year	$F_{(2,35)} = 0.40$	0.6700
	Interaction	$F_{(4,35)} = 1.14$	0.0370
Basal Area	Plot	$F_{(2,35)} = 5.72$	< 0.0001
	Year	$F_{(2,35)} = 3.15$	0.0140
	Interaction	$F_{(4,35)} = 0.86$	0.5740

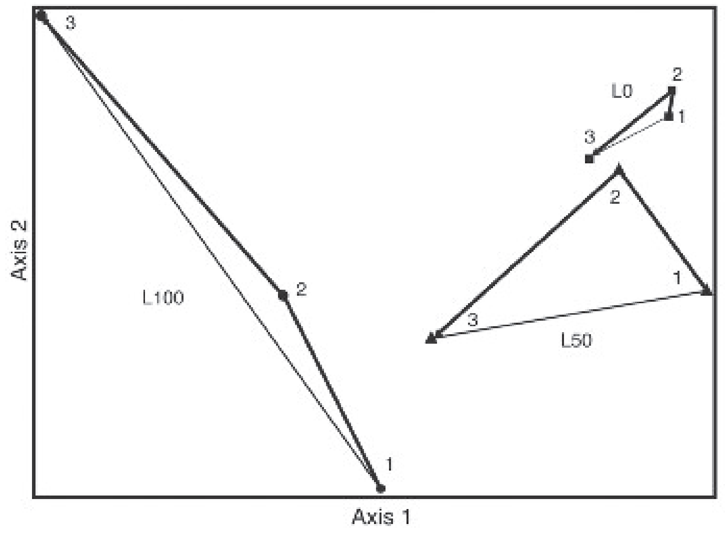

Fig. 4. First two axes of the PCA diagram of main plot vegetation traits. Arrows and bold lines show successional trajectories from 2008 to 2011 (numbers 1 to 3). Variance explained by the first PCA axis was 69.7 %.

(2) increased below-ground competition for soil nutrients and water; (3) huge cushions of recalcitrant litter and (4) restricted access to seed dispersers. The plantation canopy reduced incoming irradiance by ≈ 75 %, which repressed stem density and BA. Species richness was less affected by augmented irradiance, suggesting that species already present as seeds/seedlings, but suppressed by shade, were released after clearing, or that recruitment of a similar assemblage of species dispersed by animals or wind did take place. Although vegetation traits responded to plot thinning, it was considerably less effective in promoting colonization. Low light availability is recognized as the primary barrier for restoration in pine plantations (Ashton, Gamage, Gunatilleke, & Gunatilleke, 1997; Gómez-Aparicio et al., 2009; De Abreu, de Assis, Aguirre, & Durigan, 2011; Ashton et al., 2014), but canopy removal also has secondary deterring effects as a probable cause of water stress due to higher air temperature and lower humidity, which lead to higher evaporative demands. Another negative effect of canopy removal is the increased vulnerability to opportunistic species, such as the locally important alien tree *Syzigium jambos* (rose-apple) (Baruch & Nozawa, 2014). However, by the end of this study, none had emerged in the experimental plots.

Plantation soils were unfertile, and when combined with low irradiance, restricted the performance of prospective colonizers. Experimental fertilization partially reversed this limitation increasing stem density and BA. Unimpeded rainfall impact in the cleared plot might have caused some nutrient leaching and reduced the effect of the fertilization treatment. Pine clearing and thinning possibly diminished competition for soil nutrients, but a longer study is required for confirmation. At our site, soil oligotrophy was caused by a combination of historical low soil fertility, immobilization of nutrients in the large and fast growing pine biomass (Berthrong, Jobbagy, & Jackson, 2009), and by litter recalcitrance to decomposition delaying nutrient cycling, all common traits of pine plantations (Cavalier & Tobler, 1998; Craine & Orians, 2004; Gómez, Paolini, & Hernández, 2008; León, González, & Gallardo, 2011). Competition for soil water was probably another barrier to colonizers, considering that ~25 % of rainwater was retained and dissipated by the pine canopy, and that water shortage occurs periodically, such as during the 2009 dry season. Water shortage and elevated evaporative demand in the cleared plot might have desiccated seedlings, decreasing recruitment.

Dense pine canopies deposit thick cushions of leaf litter. The removal of this litter, either by fire or raking, significantly increased stem density but, unexpectedly, decreased BA. This pine needle layer reduces recruitment by hindering germination and/or seedling emergence physically as shown experimentally in the studied plantation (Bueno & Baruch, 2011) and elsewhere (Izhaki, Henig-Sever, & Neeman, 2000; Dodson, Peterson, & Harrod, 2008; Fernández et al., 2006; Navarro-Cano, Barberá, & Castillo, 2010) or through allelopathic effects (Nissanka et al., 2005; Guerrero & Bustamante, 2007; Fernández et al., 2006). The desirable removal of the needle litter is challenging as fire could damage the seed bank and volatilize soil nutrients while raking is extremely arduous.

Proximity to seed source sped up colonization in the cleared plot. Twenty (42.5 %) of the 47 species recorded thrive in the neighbouring montane forest (Baruch & Nozawa, 2014). Proximity to native vegetation is one of the major factors influencing restoration success (Zanne & Chapman, 2001; Chazdon, 2003; Ashton et al., 2014) and it was a main factor considered in the selection of the study site. Although Caribbean pine crowns are unattractive to bird and bat dispersers (Keenan et al., 1997; Goodale et al., 2014), plot clearings appeal to those feeding on the fruits of the early colonizers (e.g. the shrub *Clidemia hirta* in the study site; Navas, 2010), which may disperse other tree seeds into these cleared plots. It is important to point out that despite the negative effects on succession discussed above; under certain circumstances a densely sown plantation might provide some benefits for restoration such as preventing understory pine recruitment and impeding invasive species encroachment.

We conclude that light availability was the main limitation to succession which overcame the effects of the other experimental factors of this study. By the end of the fourth year, the cleared plot showed the largest responses in all traits (three times higher stem density and BA and up to twenty times higher species richness) as compared to the thinned and control plots. The removal of this barrier to recruitment and growth resulted in a marked response of vegetation which appears to follow a successional trajectory towards the local montane forest. The assisted passive restoration applied here could be the strategy of choice to increase biodiversity while maintaining the protective services to the USB campus and to similar plantations. We recommend that pine clearing should start with small patches, close to the native seed source, followed by 3 to 4 years of stabilization for colonizer recruitment and establishment. Gradually, this clearing-stabilization cycle would generate areas at different successional stages increasing local biodiversity and maintaining the protective role of the former plantation. This approach is low cost and can be conducted by unskilled workers or volunteers with few materials, but strict fire protection plus control of exotic invaders, must be effective.

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RESUMEN

¿Cuáles son los factores que limitan la colonización vegetal en una plantación de pino tropical? En los trópicos, las plantaciones de pino se emplean comúnmente para proteger laderas erosionadas. Este es el caso de la plantación de *Pinus caribaea* que resguarda el campus de la Universidad Simón Bolívar en Caracas (Venezuela) de los deslaves de lodo. Sin embargo, el inadecuado manejo

de la plantación está conduciendo a su rápido deterioro. La opción más adecuada para mantener el papel protector de la plantación es la restauración dirigida hacia una sucesión similar a la del bosque montano vecino. Mediante manipulaciones experimentales nos proponemos determinar cuáles son los factores que bloquean la sucesión secundaria e investigar sus efectos específicos. Dentro de las limitaciones impuestas por el reducido tamaño de la plantación y su rol protector, aquí analizamos los efectos de la reducida radiación solar y fertilidad del suelo, la acumulación de acículas de pino y el acceso a la fuente de semillas para la restauración. La disponibilidad de radiación solar se varió cortando y entresacando los pinos de parcelas de 800 m^2. Los tratamientos de fertilidad y la remoción de acículas (por fuego y manualmente) se realizaron en subparcelas replicadas dentro de las parcelas principales. Los suelos se analizaron fisicoquímicamente, se monitoreo el microclima y, durante 4 años, se censó la densidad, el área basal y la riqueza de especies de los elementos leñosos en las parcelas. Los resultados muestran que el acceso a la radiación solar fue el factor principal que influyó sobre la colonización y crecimiento de nuevos individuos en las parcelas con diversos grados de interacción con los sub-tratamientos. Al finalizar el cuarto año, la parcela totalmente deforestada mostró las respuestas más elevadas (tres veces superior en cuanto a densidad y área basal y hasta veinte veces mayor en cuanto a riqueza de especies) comparada con las parcelas control y parcialmente deforestada. Las principales especies leñosas colonizadoras fueron: *Croton megalodendron*, *Ocotea fendleri* y *Clusia* spp., todas ellas dominantes en el bosque montano vecino. Concluimos que este estudio pionero muestra que el aclareo total de parcelas pequeñas, repetido en ciclos de 3-4 años es apropiado para proyectos de restauración similares. Así se obtendría un mosaico de vegetación en diferentes estadios sucesionales que mantienen el papel protector de la cubierta vegetal e incrementando la biodiversidad local.

Palabras clave: acículas, limitación lumínica, *Pinus caribaea,* restauración pasiva, Venezuela.

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