

The effect of calcium on the growth of native species in a tropical forest hotspot

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Recovering of degraded areas depends not only on the choice of native species to be planted, but also on the requirements of planted seedling species in terms of soil fertility, mainly in tropical areas. This study aims to assess the effects of calcium (Ca) and soil base saturation (V%) on the growth of seedlings of eight tree species native to the Atlantic Forest biome and commonly used in restoration plantings in the study region. Seedlings were grown in a greenhouse over a period of four months in Haplic Arenosol dystric soil with low calcium content and high aluminum saturation, and were subjected to four different treatments: (i) control; (ii) lime addition until V%=40 (V40); (iii) lime addition until V%=70 (V70); (iv) addition of calcium chloride and magnesium until V%=70 (VMg70). On average, seedlings treated only with lime (V40 and V70) gave similar results, showing an increase in both shoot and root dry plant biomass. Different absorption by species belonging to different successional groups were observed. Pioneer and early secondary species showed similar behavior regarding nutrient use efficiency. Seedling fertilization increases the chances of success of restoration plantings in degraded areas by favoring seedling biomass gain and nutrient absorption, and increasing overall V% through lime fertilization. The patterns for pioneer and secondary species found in this study could contribute to decision making in restoration projects and to native seedling production of white-sand forest native species.

Keywords: Tree Species, Plant Nutrition, Liming, Nutrient Absorption Efficiency, Ecological Restoration

Introduction

The science and practice of ecological restoration have significantly advanced in the last decades. Most of the research and monitoring of areas under restoration prioritize the analysis of vegetation parameters (i.e., composition, structure, and function), while the soil compartment is rarely analyzed, though soil is considered an indicator of successful restoration (Ruiz-Jaen & Aide 2005, Viani et al. 2017). Little is known about soil influence in the success of forest restoration plantings and its interactions with planted seedlings (Ruiz-Jaen & Aide 2005, Melo et al. 2013, Perring et al. 2015).

Currently, more than half of the remaining tropical forests are highly-productive second-growth forests distributed over nu-

trient-poor and naturally acidic soils, where most of the nutrient pool lies in the biomass and is maintained through nutrient recycling (Jordan & Herrera 1981, Fujii 2014, Martins et al. 2015, Sayer & Banin 2016, Nagy et al. 2017). When vegetation is removed, most nutrients stored in the biomass are lost and litterfall is interrupted, thus halting nutrient cycling and making the soil as the only source of nutrients (Uriarte et al. 2015). Nutrient availability in soils increase as succession advances and forest structure develops, therefore forest and soil development are tightly linked in forest restoration and succession (Paul et al. 2010). Compromising soil nutrient availability may arrest forest succession and increase the chance of failure in restoration projects.

Soil chemical degradation is common in highly weathered tropical soils, compromising its quality, reducing macro- and micro-nutrients and increasing aluminum concentrations due to pH reduction. When associated to Al toxicity, low calcium concentrations can hinder root growth (especially in deeper soil layers), leading to low plant growth rates and possibly the failure of reforestation projects in tropical forest ecosystems (Uroz et al. 2014, Chazdon 2014, Jager et al. 2015, Lal 2015). Other studies have demonstrated that calcium addition can promote aboveground biomass gains while reducing root development, which indicates complex relationships of soil fertility and allocation of plant biomass (Fahey et al. 2016, Wright et al. 2011).

Most studies on soil properties during ecological restoration involve nutrient enrichment by manipulating leaf litter and the dynamics of P and N along the succession, while calcium and aluminum are rarely analyzed (Kaspari et al. 2008, Wood et al. 2009, Wright et al. 2011, Yavitt et al. 2011, Amazonas et al. 2011, Fahey et al. 2016, Sayer & Banin 2016). Calcium is regarded as one of the limiting nutrients in tropical forests, being essential for root structure and osmotic processes (White 1998), but possibly leached from soil due to the high rainfall. Since tropical soils usually contain high aluminum concentrations, this element may interfere in nutrient absorption.

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Tab. 1 - Mean \pm standard deviation of soil chemical analyses of the initial soil conditions and treatments designed in this study. (OM): organic matter; (H+Al): potential acidity; (SB): sum of bases; (CEC): cation exchange capacity; (V) base saturation; (m): aluminum saturation; (initial): soil sample before treatments; (Control, V40, V70, VMg70): mean values of the eight native tree species in each treatment at the end of the experiment. The results of the soil analysis refer to the contents available in solution and also the exchangeable contents adsorbed to soil colloids for calcium, magnesium and potassium.

Variables	Unit	Initial	Treatments (Final)			
			Control	V40	V70	VMg70
P	mg dm ⁻³	1.0 \pm 0.5	5.0 \pm 0.8	5.0 \pm 0.8	5.0 \pm 1.2	6.0 \pm 1.8
OM	g dm ⁻³	16.0 \pm 1.2	17.0 \pm 2.8	18.0 \pm 2.6	16.0 \pm 2.1	16.0 \pm 1.5
pH	CaCl ₂	3.6 \pm 0.1	4.1 \pm 0.1	4.1 \pm 0.1	4.6 \pm 0.1	4.1 \pm 0.1
K	m mol _c dm ⁻³	0.3 \pm 0.1	0.8 \pm 0.2	0.7 \pm 0.2	0.7 \pm 0.2	0.7 \pm 0.2
Ca	m mol _c dm ⁻³	3.0 \pm 0.5	4.0 \pm 1.3	4.0 \pm 0.7	6.0 \pm 1.1	6.0 \pm 1.1
Mg	m mol _c dm ⁻³	1.0 \pm 0.4	2.0 \pm 0.5	3.0 \pm 0.5	4.0 \pm 0.6	3.0 \pm 0.7
H+Al	m mol _c dm ⁻³	13.0 \pm 1.5	17.0 \pm 1.1	16.0 \pm 0.5	13.0 \pm 1.0	17.0 \pm 1.5
Al	m mol _c dm ⁻³	3.2 \pm 0.2	2.7 \pm 0.6	2.1 \pm 0.3	1.2 \pm 0.2	1.9 \pm 0.3
SB	m mol _c dm ⁻³	4.3 \pm 0.6	7.3 \pm 1.7	7.8 \pm 1.0	10.6 \pm 1.4	9.5 \pm 1.6
CEC	m mol _c dm ⁻³	17.3 \pm 1.5	24.6 \pm 2.0	23.5 \pm 1.1	23.7 \pm 1.5	26.0 \pm 2.2
V	%	25.0 \pm 2.5	29.0 \pm 5.1	33.0 \pm 2.9	45.0 \pm 3.9	36.0 \pm 4.4
m	%	43.0 \pm 3.3	28.0 \pm 7.3	21.0 \pm 3.8	10.0 \pm 2.3	17.0 \pm 6.7
S	mg dm ⁻³	5.0 \pm 1.0	12.0 \pm 1.7	11.0 \pm 1.8	11.0 \pm 2.9	13.0 \pm 3.7

Species native to tropical forests have a wide range of response to different levels of soil fertility, soil acidity, base saturation and aluminum saturation. These species-specific ranges vary in function of life-history traits, adaptation to local fertility and life stage (Gonçalves et al. 1992, Furtini et al. 2000, Sayer & Banin 2016). The higher the plant growth rate, the higher its sensibility to acidity, which influence (with some exception) the plant balance of Ca, Mg and P (Furtini et al. 2000). Several studies have demonstrated that trees and forest structure contribute to the retention of several nutrients within the system, such as P, N and Ca (Sullivan et al. 2014).

Recent global agreements are increasing the demand for restoration activities (Suding et al. 2015). In this context, there is an

urgent need to investigate how edaphic conditions affect nutrient availability in the early development stages of native seedlings used for forest restoration plantings. Our study aims to analyze the effect of calcium and soil base saturation on biomass gain and nutrient use in seedlings of eight native tree species commonly used for restoration in our study region. We expect that: (i) biomass accumulation and nutrient use will vary among seedling species according to their successional group, with pioneer trees gaining more biomass and absorbing more nutrients than non-pioneers; (ii) soil treatments with higher base saturation (V%) will favor seedling biomass gain; (iii) species with higher biomass gain will absorb more nutrients.

Materials and methods

The Haplic Arenosol (dystric) soil used in our experiment was collected in the county of Caraguatatuba, São Paulo State, Brazil (Tab. 1), in a white-sand coastal forest (Restinga forest). This forest formation belongs to the Atlantic Forest biome (Fig. 1) – one of the richest and most threatened hotspots in the world (Laurance 2009) – and usually develops over nutrient-poor marine substrates originated in the Quaternary. These white-sand forests have been historically deforested since the early stages of colonization in Brazil, and are still threatened today, mainly by the real-estate market. Additionally, the intrinsic Haplic Arenosol (dystric) characteristics of these forests, such as sandiness, low fertility (V% < 50%), high acidity and flooding, limit tree growth and pose a challenge for forest restoration in these areas (Marques et al. 2015, IUSS Working Group 2015).

Soil was collected in the 20-40 cm deep soil layer, which typically shows low concentrations of P, K, Ca and high Al saturation, indicating severe limitations to plant growth. Such conditions were adequate to test native seedling growth limitations in this study (Marques et al. 2015).

Soil samples were air dried, sieved through a 2 mm sieve and characterized by routine chemical analysis, according to the methods described by Raji Van et al. (2001). P, K, Ca and Mg contents were extracted by ion exchange resins and quantified by flame emission photometry (K) and by atomic absorption spectrophotometry (P, Ca, and Mg). We determined organic matter following the Walkley-Black method, after oxidation with a 0.167 mol L⁻¹ potassium dichromate (K₂Cr₂O₇) solution, in the presence of 5 mol L⁻¹ H₂SO₄. The excess of K₂Cr₂O₇ was titrated with Fe²⁺ ions from a standardized solution of ferrous ammonium sulfate. Soil pH was potentiometrically measured in 0.01 mol L⁻¹ CaCl₂ (1:2.5 soil:solution ratio). We extracted soil po-

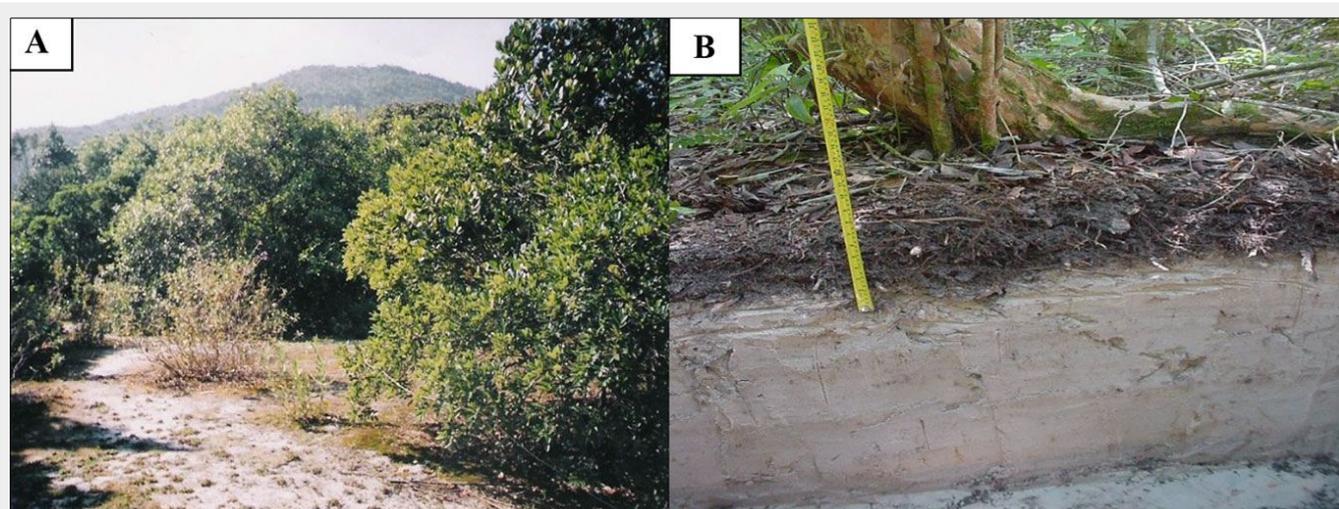


Fig. 1 - Atlantic Forest biome in Caraguatatuba, São Paulo State, Brazil. (A): white-sand coastal forest (Restinga forest); (B): Haplic Arenosol (dystric). Photos: José Carlos Casagrande.

tential acidity (H+Al) by the 0.5 mol L⁻¹ calcium acetate solution at pH 7.0. We extracted exchangeable Al content by 1 mol L⁻¹ KCl solution and determined it by titration with 0.025 mol L⁻¹ ammonium hydroxide solution. We calculated the following parameters: (i) sum of bases, SB = Ca+Mg+K; (ii) total cation exchange capacity, CEC = Ca+Mg+K+(H+Al); (iii) base saturation, V% = (SB/CEC) × 100; (iv) aluminum saturation, m% = (Al/SB+Al) × 100. We extracted S content by 0.01 mol L⁻¹ CaH₂PO₄ solution and determined it by turbidimetry.

The experiment was conducted at the Federal University of São Carlos (UFSCAR), Araras, São Paulo State, Brazil, where the climate is mesothermal with hot and rainy summers and cold dry winters (Cwa – Koppen); average annual temperature is 21.4 °C and annual rainfall is 1448.8 mm. All the following analyses were carried out at the Soil Fertility Laboratory of the University.

Limestone (hereafter “lime”) was applied to the collected soil as pure calcium and magnesium carbonate in the proportion of 3:1. The following treatments were designed: (i) control (no lime); (ii) V40 (lime for V%=40); (iii) V70 (lime for V%=70); (iv) VMg70 (calcium chloride and magnesium Ca:Mg = 4.33:1, to reach levels of Ca and Mg equivalent to V%=70, keeping soil pH unaffected). In treatment VMg70, we incorporated 0.99 g and 0.33 g of CaCl₂ and MgCl₂, respectively, in each vase.

We used 3 × 10³ m³ polyethylene vases with three liters of soil each. All treatments received a solution of nutrients containing N, P, K, S, B, Cu, Fe, Mn, Mo and Zn. These nutrients were added according to the results of soil analysis and fertilization recommendations obtained from the Technical Bulletin 100 for tree species of the Atlantic Forest (Raij Van et al. 1996). The sources of these nutrients were urea, monocalcium phosphate, ammonium sulfate, boric acid, copper sulfate, manganese, zinc and sodium molybdate.

Native seedlings (2-3 cm in height) of Atlantic tropical forest trees were provided by a plant nursery located in the municipality of Ibaté (located at 98 km from the experiment site). One seedling was planted per vase. The tree species used and their successional group are listed in Tab. 2. The seedlings were watered daily by a sprinkler system for 6 minutes, previously calculated to maintain appropriate moisture content (25%). We also weekly rotated vase position in each block clockwise.

After four months, plants were removed from their vases and dried at 65 °C for 72 hours. Shoot and root biomass were separated, grinded and weighed. We quantified shoot and root biomass dry weight, macronutrient absorption and use efficiency. To determine macronutrient content, shoot and root samples were washed in distilled water and dried in a forced-air oven at 65 °C until they reached constant mass. After drying, the plant tissue was weighed, passed through Wiley-type mill

Tab. 2 - The eight native species native used in this study and their successional group.

Species	Family	Successional Group
<i>Cecropia pachystachya</i> Trécul	Urticaceae	Pioneer (P)
<i>Lithraea molleoides</i> (Vell.) Engl.	Anacardiaceae	
<i>Schinus terebinthifolius</i> Raddi	Anacardiaceae	
<i>Cordia superba</i> Cham.	Boraginaceae	Secondary (S)
<i>Cytharexylum myrianthum</i> Cham.	Verbenaceae	
<i>Maclura tinctoria</i> (L.) D. Don ex Steud.	Moraceae	
<i>Prunus sellowii</i> Koehne	Rosaceae	
<i>Psidium myrtoides</i> O. Berg	Myrtaceae	

and digested by sulfuric solubilization for determination of N, and by nitric-perchloric mixture following the methodology proposed by Malavolta et al. (1997) for the determination of P, K, Ca, Mg, and S. We determined N using the Kjeldahl method and titration with NaOH 1 mol L⁻¹. We quantified P through photolorimetry and content was determined by flame emission photometry. The contents of Ca and Mg were determined through atomic absorption spectrophotometry and S by turbidimetry. The amount of macronutrients absorbed (AMN) by the plants was calculated by multiplying dry mass (DM) production by the macronutrient contents MC (AMN = DM × MC) of the shoot and root systems (Gonçalves et al. 1992). The nutrient use efficiency (NUE) was estimated based on the ratio of dry plant mass (DM) divided by the amount of nutrients absorbed (AMN), both in milligrams (Gonçalves et al. 1992).

The experimental design consisted of a random block design with four treatments and eight native tree species, with six repetitions, summing 192 vases. We used the ANOVA procedure to analyze dry biomass, and treatment means were compared by the post-hoc Tukey's test ($\alpha=0.05$). Considering the group of nutrients (N, P, K, Ca, Mg and S) as response variables, we carried out a multivariate analysis of variance (MANOVA) for the four following metrics: shoot and root nutrient absorption and shoot and root nutrient use efficiency. In order to investigate if species of different successional groups differed regarding nu-

trient absorption and use efficiency, we employed four tests: Wilks, Pillai, Hotelling-Lawley and Roy. When the hypothesis of mean vector similarity was rejected for a given group, the means that caused rejection were identified as mean vectors that differed from the others; in such cases, Bonferroni's confidence intervals were established (Johnson & Wichern 2007). We carried out all the analyses using the R software version 3.0.1 (R Core Team 2015).

Results

On average, treatments that used only lime to increase the sum of bases (V40 and V70) gave similar results and increased both shoot and root dry biomass (Tab. 3, Tab. 4). In VMg70, we added enough calcium and magnesium to increase V%=70 without affecting pH (Tab. 1); nevertheless, seedlings in this treatment had lower biomass accumulation than V40 and V70 (Tab. 3, Tab. 4). We observed differences in the production of dry biomass among species of the same ecological group: *Schinus terebinthifolius* showed the highest values of shoot dry biomass (Tab. 3), while high values of root dry biomass were observed for *S. terebinthifolius*, *Cecropia pachystachya*, *Cytharexylum myrianthum* and *Psidium myrtoides* (Tab. 3, Tab. 4).

We also observed different absorption by species belonging to different successional groups (Tab. 5). Early successional species showed higher nutrient absorption, except for N in shoot biomass, and N and P in root biomass (Tab. 6). Overall, we observed that

Tab. 3 - Dry shoot biomass production (g) of eight native tree species under different fertilization treatments. Means followed by the same letter do not significantly differ ($p>0.05$) across lines (uppercase letters) or columns (lowercase letters). (Control): no lime; (V40): lime addition until V% = 40; (V70): lime addition until V% = 70; (VMg70): calcium chloride and magnesium addition until equivalent Ca and Mg reach V% = 70.

Successional Group	Species	Control	V40	V70	VMg70	Averages
Pioneer	<i>C. pachystachya</i>	5.1 ^{abA}	5.0 ^{abA}	4.8 ^{bA}	4.5 ^{abA}	4.9 ^b
	<i>L. molleoides</i>	2.1 ^{cdB}	2.8 ^{bcAB}	4.1 ^{bA}	2.3 ^{bcAB}	2.8 ^{bcd}
	<i>S. terebinthifolius</i>	6.9 ^{aA}	6.6 ^{aA}	8.3 ^{aA}	6.6 ^{aA}	7.1 ^a
Secondary	<i>C. superba</i>	1.9 ^{cdA}	2.7 ^{bcA}	2.7 ^{bcA}	2.5 ^{bcA}	2.5 ^{cd}
	<i>C. myrianthum</i>	3.8 ^{bcAB}	5.3 ^{abA}	5.4 ^{bA}	3.4 ^{bcB}	4.5 ^{bc}
	<i>M. tinctoria</i>	2.7 ^{bcdAB}	3.8 ^{bcAB}	4.4 ^{bA}	2.3 ^{bcB}	3.3 ^{bc}
	<i>P. sellowii</i>	0.7 ^{dA}	1.2 ^{cA}	0.7 ^{cA}	0.7 ^{cA}	0.8 ^d
	<i>P. myrtoides</i>	3.7 ^{bcA}	4.6 ^{abA}	3.8 ^{bA}	3.4 ^{bcA}	3.9 ^{bc}
-	Averages	3.4 ^B	4.0 ^A	4.3 ^A	3.2 ^B	-

Tab. 4 - Dry root biomass (g) of eight native tree species under different fertilization treatments. Means followed by the same letter do not significantly differ ($p > 0.05$) across lines (uppercase letters) or columns (lowercase letters). (Control): no lime; (V40): lime addition until $V\% = 40$; (V70): lime addition until $V\% = 70$; (VMg70): calcium chloride and magnesium addition until equivalent Ca and Mg reach $V\% = 70$.

Successional Group	Species	Control	V40	V70	VMg70	Averages
Pioneer	<i>C. pachystachya</i>	4.5 ^{aA}	5.4 ^{abA}	3.8 ^{abA}	1.9 ^{abB}	3.9 ^a
	<i>L. molleoides</i>	0.7 ^{bB}	1.4 ^{dAB}	2.4 ^{bcA}	1.2 ^{bAB}	1.4 ^{bc}
	<i>S. terebinthifolius</i>	4.1 ^{aA}	4.6 ^{abcA}	5.4 ^{aA}	4.2 ^{aA}	4.6 ^a
Secondary	<i>C. superba</i>	0.7 ^{bA}	1.9 ^{cdA}	1.4 ^{bcA}	1.1 ^{bA}	1.3 ^{bc}
	<i>C. myrianthum</i>	4.0 ^{aB}	6.3 ^{aA}	5.7 ^{aA}	3.2 ^{abB}	4.8 ^a
	<i>M. tinctoria</i>	0.9 ^{bA}	1.7 ^{dA}	2.1 ^{bcA}	1.1 ^{bA}	1.5 ^{bc}
	<i>P. sellowii</i>	0.4 ^{bA}	0.6 ^{dA}	0.4 ^{cA}	0.4 ^{bA}	0.4 ^c
	<i>P. myrtoides</i>	2.9 ^{abA}	3.4 ^{bcdA}	3.3 ^{abA}	2.3 ^{abA}	3.0 ^{ab}
-	Averages	2.3 ^B	3.2 ^A	3.1 ^A	1.9 ^B	-

Tab. 5 - Bonferroni 95% confidence interval (CI) of absorption and nutrient use efficiency in shoots and roots and of nutrient use efficiency in the shoots of seedlings of the eight native species. No significant effect was found for root efficiency after multivariate analysis of variance (MANOVA). (Lower CI): lower limit of CI; (Upper CI): upper limit of CI; (*): $p < 0.05$.

Nutrient	Absorption (g kg ⁻¹)				Efficiency (%)	
	(a) Roots		(b) Shoots		(c) Shoots	
	Lower CI	Upper CI	Lower CI	Upper CI	Lower CI	Upper CI
N	-7.95	33.14	-11.75	30.88	1.06	43.30*
P	-0.35	4.38	0.45	8.52*	-276.33	182.29
K	1.42	3.98*	15.40	45.71*	-49.97	6.08
Ca	0.96	9.51*	0.81	29.35*	-37.21	69.53
Mg	2.28	15.36*	1.09	15.93*	-107.48	91.63
S	1.47	2.89*	2.25	8.16*	-347.22	32.24

pioneer species absorbed approximately two times more K and S than secondary species in shoot biomass (0.0585 g kg⁻¹ of K and 0.0105 mg kg⁻¹ of S for pioneers, 0.0280 mg kg⁻¹ of K and 0.0053 mg kg⁻¹ of S for secondary species). Similarly, pioneer species absorbed 37.6%, 38.3% and 43.5% more P, Ca and Mg, respectively, than secondary species. Roots of pioneer species absorbed, on average, 1.0, 2.0 and 3.0 times more N, Ca and Mg than secondary species, respectively.

Root nutrient-use efficiency was similar among pioneer and secondary species. Regarding shoot biomass, pioneer species were, on average, 1.5 times more efficient in the use of N than secondary species, while nutrient use efficiency of other com-

ponents was similar between successional groups (Tab. 5, Tab. 6).

Discussion

Overall, our results indicate the need to correct the soil through liming, in order to reach at least $V\%=40$. A seemingly small increase in $V\%$ (i.e., from the original $V\% = 25$ to $V\% = 40$ in the treatment V40) considerably increased shoot and root biomass. Therefore, for these species a slight increase in base saturation to $V\%=40$ will contribute to increase seedling quality, productivity and establishment, and reduce soil correction costs in forest restoration plantings as well. Fertilization is particularly important for restoration plantings in tropical degraded areas, where soils are usually

nutrient-poor (Villalobos et al. 2014, Lima-Perim et al. 2016). In acid soils, which exhibit high toxicity to aluminum and low cation exchange capacity, the availability of nutrients to plants is hindered and soil correction may favor nutrient absorption and incorporation in plant biomass, as observed in our results and many other studies (Furtini et al. 1999, Meriño-Gergichevich et al. 2010, Campos et al. 2014, Fujii 2014, Martins et al. 2015, Lima-Perim et al. 2016, Raboin et al. 2016).

Our findings corroborates with the study by Furtini et al. (2000) regarding the macronutrient accumulation and use efficiency in response to phosphorus fertilization, in which late secondary species were less sensible to fertilization. Furthermore, our results also corroborates with Sorreano (2006), who evaluated 17 tree species and showed that fast-growing species were more sensitive to the lack of nutrients and showed visual signs of deficiency faster than slow-growing species, which indicated higher nutrient demands.

The higher average nutrient absorption observed for pioneers and the higher root biomass detected for two of the three pioneer species used in this experiment (*C. pachystachya* and *S. terebinthifolius*), as well as the higher shoot biomass of *S. terebinthifolius*, are probably all related to the successional strategy of these species (Tab. 3, Tab. 4 and Tab. 6). As a consequence of higher growth rates, early successional species require, absorb and accumulate more nutrients, and respond positively and faster to fertilization (Gonçalves et al. 1992, 2008). The higher nutrient absorption of early successional species may be caused by the expansion of the root system and, consequently, the exploration of more soil (Gonçalves et al. 1992, 2008). The development of pioneer species in a degraded site ameliorate climatic and soil conditions and favors the establishment of late-successional species, effectively recuperating successional process (Trindade & Coelho 2012).

Initially, we expected that late secondary species would have higher nutrient use efficiency; however, species of different successional groups were similar regarding nutrient use efficiency. Previous studies demonstrated different nutrient use effi-

Tab. 6 - Mean values of absorption and nutrient use efficiency of shoots and roots of eight native tree species. Different letters between rows within the same plant section (shoot or roots) indicate significant differences ($p < 0.05$) between pioneer and secondary species.

Characteristic	Plant Section	Successional Group	N	P	K	Ca	Mg	S
Absorption (g kg ⁻¹)	Shoot	Pioneer	0.0490 ^a	0.0119 ^a	0.0585 ^a	0.0394 ^a	0.0196 ^a	0.0105 ^a
		Secondary	0.0394 ^a	0.0074 ^b	0.0280 ^b	0.0243 ^b	0.0111 ^b	0.0053 ^b
	Roots	Pioneer	0.0372 ^a	0.0055 ^a	0.0204 ^a	0.0115 ^a	0.0161 ^a	0.0063 ^a
		Secondary	0.0249 ^a	0.0036 ^a	0.0199 ^b	0.0050 ^b	0.0053 ^b	0.0047 ^b
Efficiency (%)	Shoot	Pioneer	107.3 ^a	422.4 ^a	84.4 ^a	137.3 ^a	272.2 ^a	462.7 ^a
		Secondary	76.7 ^b	481.9 ^a	107.4 ^a	124.2 ^a	287.0 ^a	625.9 ^a
	Roots	Pioneer	92.3 ^a	576.0 ^a	156.7 ^a	320.3 ^a	275.0 ^a	574.0 ^a
		Secondary	170.5 ^a	672.7 ^a	124.3 ^a	457.3 ^a	409.2 ^a	588.2 ^a

ciency for different species (Gonçalves et al. 1992). In the field, pioneer species showed slightly higher nutrient use efficiency for N and P than secondary species, while in greenhouses the opposite trend was observed. This contrast between field and greenhouse behavior may have occurred because pioneers in the field could intensify their physiological functions, increasing nutrient use and efficiency. Our work was carried out in nutrient poor soils, and the results obtained for N in the shoot biomass of pioneers may result also from the intensification of their physiology for this nutrient (Tab. 5). In the early stages of restoration plantings, such species may show consistent differences in nutrient use and absorption when compared to older plantings (Waring et al. 2015).

Although Brazil is a global example of native seedlings production for forest restoration and implementation of large-scale restoration programs, there is a lack of studies on white sands ecosystems (Bernardino et al. 2007, Macedo & Teixeira 2011, Coneglian et al. 2016). On the other hand, the effect of liming on soil acidity, nutrient availability and plant responses have been thoroughly reported in agricultural and silvicultural investigations (Chatzistathis et al. 2015, Tiritan et al. 2016). The few studies in the Atlantic white sand forests (*Restinga*) that evaluate liming for seedling production point out that native species show a variety of responses to liming and nutrient-poor environments and, in most cases, native species benefited from the reduction in soil acidity, as observed for the averages of treatments V40 and V70 in our study (Tab. 3, Tab. 4).

Other studies on coastal white-sand forests have reported a low vegetation resilience due to soil characteristics. Higher fertility is found in the first 10 cm of soil and, given its high leaching rates, this soil layer has a high density of fine roots for quick nutrient absorption. In these ecosystems, 70% of the root system is located in the 0-10 cm layer and 90% of the root biomass is found up to only 20 cm depth. High Al concentration in these soils hampers downward root growth (Bonilha et al. 2012). The white sand forests that were the subject of this study show structure and species richness and diversity similar to other forests established on sandy and nutrient-poor soils around the world (Lima et al. 2011).

The patterns for pioneer and secondary species found in this study could contribute to decision-making in restoration projects and to native seedling production of white-sand forest species. However, the existence of species-specific responses has to be taken into consideration (Jamaluddin et al. 2013).

Conclusion

Seedling fertilization increases the chances of success of restoration plantings in degraded areas by favoring native seed-

ling biomass gain and nutrient absorption, and increasing overall soil base saturation through lime fertilization. Although nutrient use efficiency was similar among the studied species, nutrient absorption and biomass gain were related to the successional role of each species, with pioneers showing higher rates. Our results point out the need of further research in this field, as scientific knowledge about the fertilization of native species and their potential to convert nutrients in biomass is still scarce, particularly in field experiments (Gonçalves et al. 2012). Increasing our knowledge on the specific requirements of native forests, particularly in nutrient absorption, is an important step to create guidelines for fertilization in reforestation projects and obtain higher seedling development in restoration plantings, thus reducing maintenance costs and promoting a quick recover of ecological processes of restoration areas.

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Authors' contributions

DTGB: conducted the experiment and leaded the writing of the manuscript; JCC: tutor of the first author and contributed to the writing of the manuscript and discussion of the results; MRS: contributed to the writing of the manuscript and discussion of the results; SDS and CB: carried out statistical analysis of the data; RGC: contributed to the writing of the manuscript and discussion of the results.

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