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Functional traits of tree saplings and adults in a tropical cloud forest restoration context

Atributos funcionales de árboles juveniles y adultos en el contexto de restauración del bosque de niebla

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Abstract
Background: The use of tree species' functional traits is a promising approach in forest restoration. However, some traits may change during ontogeny.
Questions: Does intraspecific variation in functional traits occur between sapling and adult stages? Do groups of species can be delimited based on functional traits regardless of their ontogenetic stage?
Study sites and dates: Cloud forest restoration, Veracruz, Mexico, 2016.
Methods: Saplings and adults of eight native tree species in different age plantations were measured for leaf area (LA), specific leaf area (SLA), stomatal density (SD), foliar nutrient content (C, N, P) and relative growth rate (RGR). Wood density (WD) was measured for adults. Data were analyzed using linear mixed models and principal component analysis (PCA).
Results: Overall, SLA was higher in saplings than in adults. A few species showed intraspecific variation for LA (three species), SD (three) and foliar N content (one). Species with high WD (*Quercus* spp.) and intermediate WD (*e.g.*, *Liquidambar styraciflua*) tended to have lower LA and SLA, and higher SD. Species with low WD (*e.g.*, *Heliocarpus donnellsmithii)* had high SLA, RGR, and N content. PCA highlighted that saplings and adults of a same species were close to each other within the ordination space.
Conclusions: Intraspecific variation between saplings and adults was small for most traits (except SLA) in comparison to differences across species. Therefore species trait values (measured in individuals of any age) could be a useful tool to characterize groups of species during the forest restoration trajectory.
Key words: Growth rate, leaf area, specific leaf area, stomatal density, wood density.

Resumen
Antecedentes: Usar atributos funcionales de especies arbóreas es un enfoque prometedor en restauración ecológica. Aunque algunos atributos pueden cambiar durante la ontogenia.
Preguntas: ¿Existe variación intraespecífica en atributos funcionales entre árboles juveniles y adultos? ¿Se pueden delimitar grupos de especies basados en atributos funcionales independientemente de su ontogenia?
Sitios y fecha de estudio: Restauración de bosque de niebla, Veracruz, México, 2016.
Métodos: A juveniles y adultos de ocho especies nativas en plantaciones de diferente edad se les midió área foliar (AF), área foliar específica (AFE), densidad estomática (DE), nutrientes foliares (C, N, P), y tasa de crecimiento relativa (TCR). Densidad de la madera (DM) se midió en adultos. Los datos se analizaron utilizando modelos lineales mixtos y análisis de componentes principales (ACP).
Resultados: En general, AFE fue mayor en juveniles que en adultos. Algunas especies mostraron variación intraespecífica para AF (tres especies), DE (tres) y N (una). Especies con DM alta (*Quercus* spp.) e intermedia (*e.g.*, *Liquidambar styraciflua*) tuvieron AF y AFE bajos y DE alta. Especies con DM baja (*e.g.*, *Heliocarpus donnellsmithii*) tuvieron AFE, TCR y N altos. ACP destacó que juveniles y adultos de una misma especie estaban cercanos dentro del espacio de ordenación.
Conclusiones: Las diferencias intraespecíficas entre juveniles y adultos para atributos funcionales (excepto AFE) fueron menores que las diferencias entre especies. Consecuentemente, los valores de los atributos de cada especie (medidos en individuos de cualquier edad) podrían ser una herramienta útil para caracterizar grupos de especies durante la trayectoria de restauración forestal.
Palabras clave: Área foliar, área foliar específica, densidad de madera, densidad estomática, tasa de crecimiento.

The active ecological restoration of degraded forest areas has mainly been conducted through a process of planting native tree species and assessing growth and survival in response to environmental variables. The use of the functional traits of trees has increasingly been studied as a promising approach to select species for forest restoration (Martínez-Garza *et al.* 2005, Flores *et al.* 2014, Ostertag *et al.* 2015, Gustafsson *et al.* 2016, Toledo-Aceves *et al.* 2017). Functional traits have been described as the main characteristics related to the reproduction, survival, growth and fitness of plant species, based on physiological, morphological and phenological characteristics (Violle *et al.* 2007). Functional traits are already in use as indicators of success in ecological restoration practices (Martínez-Garza *et al.* 2013, Ostertag *et al.* 2015).

Environmental filtering to restore a community may act differentially on seedlings, saplings and adult trees, and there are several studies highlighting the importance of incorporating ontogenetic trait variation into approaches that use plant functional traits (Poorter 2007, Spasojevic *et al.* 2014). Functional traits known to be good predictors of demographic rates and fitness in the regeneration stage are also apparently good predictors of plant performance in the post-regeneration stage across a wide range of Neotropical forests (Poorter *et al.* 2008). Some studies show how traits may differ with plant age-size (Gibert *et al.* 2016). Other studies have found variation in functional leaf traits at different ontogenetic phases in the restoration context (*e.g.*, Martínez-Garza & Howe 2005, Lapok *et al.* 2017).

Tropical montane cloud forest (TMCF) is remarkably diverse in terms of its physiognomy and tree species composition but is particularly threatened by habitat destruction and global change (Bruijnzeel *et al.* 2010, Williams-Linera *et al.* 2013). Ecological restoration is important for preserving forest biodiversity and ecosystem services; however, restoration takes decades and the existing reports are frequently based on seedlings and saplings in recently established plantations, and uncommonly on adults in old restoration sites (Wortley *et al.* 2013). In the TMCF region of central Veracruz, Mexico, several ecological restoration sites were established since 1998 in recently abandoned pastures using early and late successional native tree species (Williams-Linera *et al.* 2016). The microenvironmental conditions prevalent in young plantations are more similar to those of large forest gaps or open areas, with lower canopy cover, higher light levels and lower soil water content. In contrast, in middle-age plantations, conditions are more akin to those found in secondary forests (Alvarez-Aquino *et al.* 2004, Muñiz-Castro *et al.* 2015).

In this study, young and middle-aged plantations of native tree species were used to compare the functional traits of saplings and adults of several species with different wood density in relation to growth rates. Plant relative growth rate is an intrinsic response of particular species in an assemblage (Rüger *et al.* 2012, Gibert *et al.* 2016) and has been used to compare the performance of different species in restoration assays. Leaf characteristics are highly variable but have been related to the ability of the plant to survive and grow and compete for light (Bongers & Popma 1990, Wright *et al.* 2004, Poorter *et al.* 2008). Furthermore, leaf and wood traits appear to be good proxies for physiological rates and are correlated with relative growth rate (Poorter & Bongers 2006, Janse-ten Klooster *et al.* 2007, Poorter *et al.* 2008, Gibert *et al.* 2016). We selected easily measurable functional traits (leaf area (LA), specific leaf area (SLA), stomatal density (SD), and foliar nutrients (C, N, P)) that have been demonstrated to have predictable trends during succession and have been suggested for use in monitoring forest restoration (Martínez-Garza *et al.* 2013, Ostertag *et al.* 2015, Brancalion & Holl 2016).

The objective of this study was to evaluate the functional traits of the same tree species at the sapling (2-3 years) and adult (13-17 years) stages in ecological restoration sites in a TMCF region. We hypothesized that 1) functional traits would vary between saplings and adults, and 2) functional traits display a range of values that cause grouping of tree species regardless of the ontogenetic variation.

Materials and methods

Study sites. The study sites are located in the tropical lower montane forest region of Veracruz, Mexico (19° 30' N; 96° 57' W) between 1,280 and 1,450 m asl. The climate is mild and humid throughout the year, with three distinct seasons: a relatively dry-cool season from November to March, a dry-warm season in April-May and a wet-warm season from June to October. Annual precipitation is 1,600-1,800 mm and the mean temperature is 17-18 °C. The soil has been classified as Andosol. The dominant tree species are *Carpinus tropicalis* (Betulaceae), *Clethra macrophylla* (Clethraceae), *Liquidambar styraciflua* (Altingiaceae), *Quercus lancifolia* (Fagaceae), *Q. sartorii* (Fagaceae), *Q. xalapensis* (Fagaceae) and *Turpinia insignis* (Staphyleaceae) (Williams-Linera *et al.* 2013). In this region, five restoration plantations with native tree species were chosen (Pedraza & Williams-Linera 2003, Muñiz-Castro *et al.* 2015, Williams-Linera *et al.* 2010, 2015, 2016). The sites included plantations that were categorized as recently established or young (average age = 2.5 yr) and middle-aged (average age = 14.2 yr) (Table 1). The average distance among sites was 4.6 km. All sites were situated on slopes of 11 to 36°. Soils are volcanic in origin and > 2.5 m depth, mildly acidic (pH 5.1 to 5.6), low in extractable P (4.5 mg/kg), high in organic matter (10-20 %), with a bulk density of 0.9 to 1.1 g/cm^3, and texture from clay to sandy-clay-loam. Because of the sites' proximity to each other, there are clear similarities in climate, physical and chemical soil characteristics and geomorphic environmental conditions. Thus, we were confident that the trait values of saplings and trees can be reliably compared.

Eight planted native tree species were selected from the five restoration sites (Table 2). All saplings were collected in young sites, and all adults were collected in middle-age sites. The sapling stage was < 10 cm diameter and < 10 m tall, and the adult stage included trees > *ca.* 10 cm diameter and > 10 m tall (Table 2).

Functional traits. Mature leaves with no herbivore damage that receive direct sunlight were collected from two branches on opposite sides of the stem or trunk with an oversized slingshot. The leaves of three saplings or three to six adults of each species were collected per site during the wet-warm season following standardized protocols (Cornelissen *et al.* 2003). The leaves were stored in black plastic bags and transported to the Laboratory of Functional Ecology at the Institute of Ecology, Xalapa, Mexico for subsequent analysis.

We selected 10 to 20 leaves from each individual. The area of each leaf (LA, cm^2), excluding the petiole, was measured in a WinFOLIA Leaf Area Meter (Software program LA2400). The leaves were oven-dried at 60 °C for at least 72 hr and dry mass determined. Specific leaf area (SLA) was calculated as leaf area divided by leaf dry mass. The leaves were then ground for analysis to determine foliar carbon, nitrogen and phosphorus. Leaf C and N were determined using the TruSpec Micro, and leaf P by digestion with HNO_3/ $HClO_4$. The samples were analyzed using standard techniques (SEMARNAT 2002).

Stomatal density (SD) was determined in two fresh leaves per species and site. At the top, center and bottom of the abaxial surface of each leaf, we applied an imprinting paste followed by clear nail polish to produce stomatal imprints. Stomatal densities were determined using a compound microscope with 20x objective from photographs and expressed as stomata/mm^2.

Wood density (WD) was determined from a core extracted from each adult tree at a height of 1.3 m above ground level with a Pressler increment borer. In the

Table 1. Characteristics of the restoration sites in the tropical montane cloud forest region of central Veracruz, Mexico, where tree saplings or adults (stage) were sampled. MAP is mean annual precipitation, MAT is mean annual temperature. Plantation is the year of plantation establishment. Age (years) and stage (adult, sapling) of the plants.

Site	Latitude N	Longitude W	Elevation (m asl)	MAP (mm)	MAT (°C)	Plantation	Age	Stage	Reference
1	19° 35' 10"	96° 57' 16.7"	1,450	1,836	16.8	2002	13	adult	1
2	19° 32' 10.1"	96° 58' 4.9"	1,450	1,669	17.9	1998	17	adult	2
3	19° 30' 52.5"	96° 59' 27.9"	1,405	1,925	17.1	2002	13	adult	1
4	19° 30' 57.5"	96° 56' 51.5"	1,370	1,621	18.5	2012	3	sapling	4
5	19° 30' 37.8"	96° 56' 43.1"	1,280	1,621	18.5	2013	2	sapling	3

Reference: 1, Muñiz-Castro *et al.* 2015; 2, Pedraza & Williams-Linera 2003; 3, Toledo-Aceves *et al.* 2017; 4, Williams-Linera *et al.* 2015.

Table 2. Tree species in tropical montane forest restoration sites in central Veracruz, Mexico. Wood density of adults (WD)**,** mean diameter (cm) and height (m) of saplings and adults. Site numbers are given in Table 1.

Species	Family	WD	Diameter (cm)		Height (m)		Site
			Sapling	Adult	Sapling	Adult	
Carpinus tropicalis (Donn. Sm.) Lundell	Betulaceae	0.55	3.8	14.7	4.6	9.5	2, 5
Heliocarpus donnellsmithii Rose	Malvaceae	0.34	8.8	12.3	4.9	10.3	1, 3, 5
Juglans pyriformis Liebm.	Juglandaceae	0.51	3.2	17.4	3.2	12.9	2, 4
Liquidambar styraciflua L.	Altingiaceae	0.55	4.8	22.8	5.3	15.4	2, 5
Myrsine coriacea (Sw.) R. Br. ex Roem. & Schult.	Primulaceae	0.51	3.6	9.8	3.4	9.7	1, 3, 5
Quercus germana Schltdl. & Cham.	Fagaceae	0.74	3.1	12.5	1.8	10.6	1, 3, 5
Quercus xalapensis Bonpl.	Fagaceae	0.61	4.4	18.6	2.4	14	1, 3, 5
Trema micrantha (L.) Blume	Cannabaceae	0.51	8.4	26.4	5.6	18.5	1, 3, 5

laboratory, these cores were submerged in distilled water for three days until fully hydrated. The volume of the cores was determined by the water displacement method, and dry weight was measured after the cores had been oven-dried at 60 °C for 72 hr.

Relative growth rates (RGR) in height and diameter were estimated using published and unpublished databases from previous works conducted in different years in the same sites, species and permanently tagged individuals used in this study (Table 1, 2). We used the equation RGR = ln H_2 - ln $H_1/(t_2 - t_1)$, where H_2 and H_1 are height/diameter, and t_2 and t_1 are time in years (Hunt 1990). RGR was calculated for one period between two censuses and expressed over an interval of a year. The time span used to calculate RGR was 3-4 years for saplings and 8-10 years for adults.

Statistical analysis. Differences in leaf traits between stages were analyzed using a linear mixed model with stage as fixed effect, and sites as a random effect. To attain normality and homoscedasticity in the residuals of both models, we used a $\log_{10}$ transformation. Inspection of residuals was used to verify whether the model's assumptions had been met. WD was compared with respect to species using generalized linear model. Post hoc tests were conducted using Tukey's HSD. Analyses were conducted using the statistical platform of R version 3.4.2 (https://www.R-project.org/ 2017). A principal component analysis (PCA) was run to summarize and to visualize the main trends of sapling and adult tree species, and the relationships with foliar traits and RGR. The PCA was run in the PC-ORD software (McCune & Grace 2002).

Results

Leaf area showed significant stage × species interaction, and differences among species, but LA was similar between saplings and adults (Figure 1A, Table 3). LA of *H. donnellsmithii* was higher for saplings than for adults, but LA of *Q. xalapensis* and *T. micrantha* was higher for adult trees. Also, LA was higher for *Heliocarpus donnellsmithii*, intermediate for four species (*e.g.*, *Q. xalapensis*), and smaller for *Trema micrantha*, *Carpinus tropicalis* and *Myrsine coriaceae* (Table 4).

Overall, SLA was higher in saplings than in adults (Figure 1B, Table 3), and there were differences among species (Table 3). SLA was higher in *H. donnellsmithii*, and lower in *Q. xalapensis*, *Q. germana* and *J. pyriformis* (Table 4).

Stomatal density displayed significant stage × species interaction and differed among species, but SD was similar in saplings and adults (Figure 1C, Table 3). *L. styraciflua* and *Q. germana* had higher SD in saplings, whereas *T. micrantha* had higher SD in adults (Table 4). Foliar C, N and P content were similar in both stages, but species differed in their foliar nutrient content (Figure 1D - F, Table 3, 4).

Wood density differed among tree species (F = 6.39, p = 0.019), with *Q. germana* and *Q. xalapensis* having the highest WD. The other species had intermediate values (*L. styraciflua*, *C. tropicalis*, *J. pyriformis*, *M. coriacea*, *T. micrantha*), while *H. donnellsmithii* had the lowest WD (Table 2).

Relative growth rate was higher for *H. donnellsmithii*, *M. coriacea* and *T. micrantha* than for the other species (Figure 2). Also, RGR was higher in saplings than in adults of those three species. RGR in height and diameter were correlated (r = 0.94, p < 0.0001), so we used RGR in height for further analysis.

The PCA based on leaf traits and RGR of tree species in the sapling and adult stages is shown in Figure 3. The first three components of PCA explained 73.3 % of the total variation. LA, SLA and leaf N content had positive loading on axis 1; leaf P content and stomata were positively related to axis 2, and RGR had positive loading on axis 3 (Table 5). *Q. xalapensis* had the highest SD and foliar P content. *H. donnellsmithii* had high LA, SLA and foliar N. The clearest pattern was more separation of saplings and adults of species (*H. donnellsmithii*, *M. coriacea* and *T. micrantha*) in the right side of axis 1 (Euclidean distance, 141, 87, 136, respectively, mean = 121.8), and less separation between stages in species towards the central part (*C. tropicalis*; *J. pyriformis*, *L. styraciflua*) and left side of axis 1 (*Q. germana* and *Q. xalapensis*) (Euclidean distance, 27, 38, 40, 46, 42, respectively; mean = 38.6) within the ordination space.

Discussion

Traits are expected to influence growth rates, depending on plant size from seedling to sapling to adult (Martínez-Garza & Howe 2005, Martínez-Garza *et al.* 2005, Gibert *et al.* 2016). Overall, we found that one foliar trait (SLA) differed across plant development stages while others, such as LA, SD and foliar nutrient content, were similar in saplings and adults. In addition, we found that LA, SLA, SD and foliar nutrient content differed among species, coinciding with observations about the broad spread of trait values across species within a site (Westoby & Wright 2006). Relationships among LA, SLA and N content have been previously reported in tropical montane and lowland forests (Wright *et al.* 2004, 2007, Lohbeck *et al.* 2013, Flores *et al.* 2014). However, the use of at least one trait (SLA or its inverse, specific leaf mass, SLM), characterized by intraspecific variability and correlated with other traits, has proved to be relevant for restoration (Martínez-Garza *et al.* 2005).

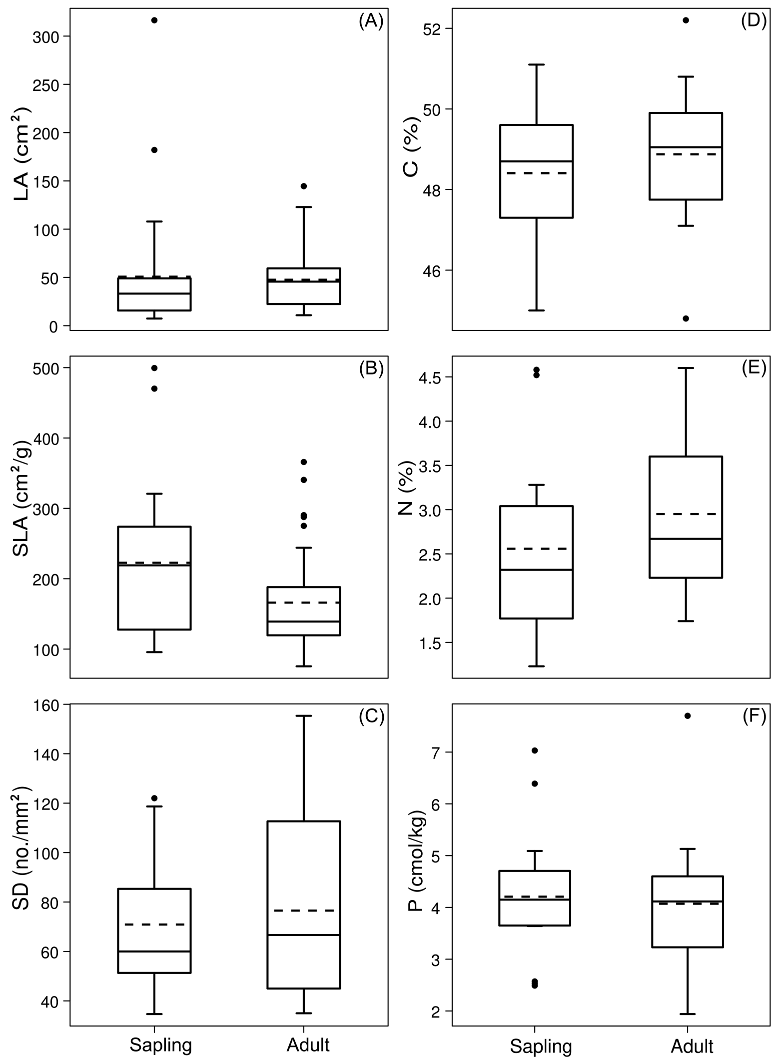

Figure 1. Boxplots of leaf functional traits measured in tree saplings and adults in tropical montane cloud forest restoration sites in Veracruz, Mexico. (A) leaf area, (B) specific leaf area, (C) stomatal density, (D) carbon, (E) nitrogen, and (F) phosphorus. The crossbar within the box indicates the median and the dotted line the mean; the length of the box represents the interquartile range of distribution, the lower and upper fences indicate the 10th and 90th percentiles, respectively, and dots represent outliers of the data.

Table 3. Results of linear mixed models used to evaluate the effect of stage (sapling, adult) on eight species in tropical montane cloud forest restoration sites in central Veracruz, Mexico. Significant effects are in boldface type.

	Stage			**Species**			**Stage × Species**		
	df	***F***	***p***	**df**	***F***	***p***	**df**	***F***	***p***
Leaf area	1, 3	2.44	0.2164	7, 39	28.87	**< 0.0001**	7, 39	3.75	**0.0034**
Specific leaf area	1, 3	23.97	**0.0163**	7, 39	27.33	**< 0.0001**	7, 39	1.78	0.1201
Stomatal density	1, 3	0.48	0.5368	7, 113	31.42	**< 0.0001**	7, 113	11.18	**< 0.0001**
Foliar C	1, 4	0.67	0.4600	7, 12	27.02	**< 0.0001**	7, 12	2.48	0.0797
Foliar N	1, 4	0.6	0.4814	7, 12	34.1	**< 0.0001**	7, 12	4.16	**0.0151**
Foliar P	1, 4	0.05	0.8299	7, 12	14.48	**0.0001**	7, 12	0.41	0.8794

Table 4. Leaf functional traits of saplings and adults of tree species in tropical montane cloud forest restoration sites in Veracruz, Mexico. Traits are leaf area (LA), specific leaf area (SLA), stomata density (SD), foliar carbon (C), nitrogen (N) and phosphorous (P). Values are mean and standard error. Boldface type denotes difference (α = 0.05) between saplings and adults within a same species. Species trait in a same column accompanied by the same letter did not differed significantly (α = 0.05).

Species	**LA (cm²)**			**SLA (cm²/g)**			**SD (no./mm²)**		
	Sapling	**Adult**		**Sapling**	**Adult**		**Sapling**	**Adult**	
Carpinus tropicalis	9.0±0.5	22.2±0.9	d	280.9±11.6	261.2±12.5	b	102±13	90±11	b
Heliocarpus donnellsmithii	**197.0±26.8**	**93.0±7.1**	a	375.9±934.7	280.5±6.5	a	58±7	60±4	de
Juglans pyriformis	55.2±2.0	59.0±4.1	b	127.6±5.4	90.6±4.1	e	52±4	57±7	de
Liquidambar styraciflua	32.4±1.7	48.3±3.4	c	169.5±5.2	154.3±10.7	d	**70±5**	**36±3**	de
Myrsine coriacea	16.0±0.8	15.0±0.8	d	245.5±2.9	157.2±4.1	c	42±4	50±4	e
Quercus germana	36.4±1.1	50.0±2.4	c	117.1±2.5	121.0±2.4	e	**94±6**	**51±6**	cd
Quercus xalapensis	**28.3±4.4**	**55.4±3.4**	c	113.0±22.7	136.4±1.8	e	112±6	134±7	a
Trema micrantha	**16.1±1.1**	**38.3±1.7**	d	253.9±6.1	131.7±3.0	c	**57±7**	**111±5**	bc
Species	**C (%)**			**N (%)**			**P (cmol/kg)**		
	Sapling	**Adult**		**Sapling**	**Adult**		**Sapling**	**Adult**	
Carpinus tropicalis	47.7±0.1	49.7±0.3	bc	1.8±0.0	2.9±0.2	d	4.7±0.1	4.3±0.7	ab
Heliocarpus donnellsmithii	48.5±0.4	48.1±0.3	bc	4.6±0.0	4.4±0.1	a	4.2±0.0	4.5±0.0	b
Juglans pyriformis	46.9±0.2	49.0±0.7	cd	2.9±0.0	2.6±0.0	bc	2.5±0.0	2.2±0.3	b
Liquidambar styraciflua	49.4±0.8	49.1±0.2	ab	1.7±0.5	2.1±0.1	d	4.5±0.6	3.2±0.2	ab
Myrsine coriacea	50.9±0.2	51.5±0.8	a	2.6±0.2	2.8±0.3	bcd	3.8±0.1	3.2±0.3	b
Quercus germana	49.4±0.2	47.5±0.2	ab	2.1±0.0	1.8±0.0	cd	3.9±0.3	4.5±0.1	b
Quercus xalapensis	49.6±0.0	50.3±0.5	ab	**1.6±0.0**	**2.8±0.5**	d	6.7±0.3	6.4±1.3	a
Trema micrantha	45.1±0.1	46.0±1.2	d	3.2±0.0	4.3±0.3	b	3.4±0.8	4.1±0.0	b

As expected, SLA was higher in the saplings since it is a trait related to ontogeny (Martínez-Garza *et al.* 2005, Jansen-ten Klooster *et al.* 2007, Spasojevic *et al.* 2014), and SLA is also the most responsive attribute to different light environments in cloud forest seedlings and saplings (Toledo-Aceves *et al.* 2017). Even though stomatal density can be affected by the availability of water and light, as well as by temperature (Loranger & Shipley 2010), and several studies have reported higher SD in leaves exposed to the sun than in shade leaves (Popma *et al.* 1992, Loranger & Shipley 2010) we found that, overall SD was similar between saplings and adults. In this study, *L. styraciflua* and *Q. germana* had a higher SD in saplings, but *T. micrantha* showed the opposite trend. Although there were no differences in LA, SD and foliar nutrient content between stages, we found a stage × trait effect in some species. This variation suggests that species respond individually displaying contrary trends and then the overall difference is not detected when all species were considered together.

While plant development stage was clearly related to SLA only, there is a consistency in the trait trends for groups of species. Considering the leaf economic spectrum (Wright *et al.* 2004), the wood economic spectrum (Chave *et al.* 2009) and RGR (Rüger *et al.* 2012, Gibert *et al.* 2016), species can be categorized into different plant strategies. The SLA and WD are expected to have a negative relationship, reflecting the continuum from fast growing, light-demanding (high SLA, low WD, higher respiration rates and higher rate of nutrient uptake) to slow growing, shade-tolerant (high WD, low SLA) species (Wright *et al.* 2007, Chave *et al.* 2009, Rüger *et al.* 2012). This trend has been observed in tropical forests, where species with high SLA have a high N content per unit leaf area, high assimilation and high RGR (Bongers & Popma 1990, Poorter *et al.* 2008, Poorter & Bongers 2006, Gustafsson *et al.* 2016). Another general relationship is that SD decreases with increasing SLA, and SLA was higher and SD lower for shade leaves than sun leaves (Bongers & Popma 1990, Loranger & Shipley 2010). The PCA showed that the intraspecific difference due to stage was small in comparison to the difference across species, since saplings and adults remained close within the ordination space.

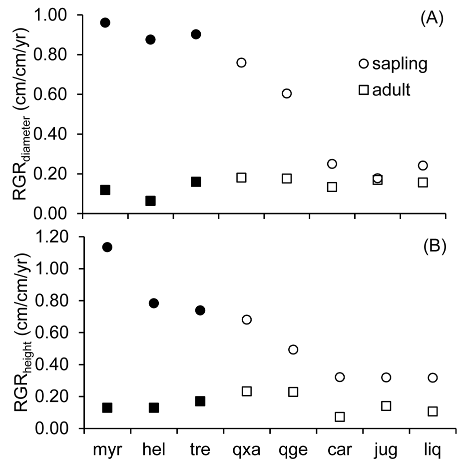

Figure 2. Relative growth rate (RGR) in (A) diameter and (B) height for the saplings (circle) and adults (square) of eight tree species in tropical montane cloud forest restoration sites in Veracruz, Mexico. Filled symbols represent pioneer species; open symbols represent non-pioneer species. myr, *Myrsine coriacea*; hel, *Heliocarpus donnellsmithii*; tre, *Trema micrantha*; qxa, *Quercus xalapensis*; qge, *Quercus germana*; car, *Carpinus tropicalis*; jug, *Juglans pyriformis*; liq, *Liquidambar styraciflua*.

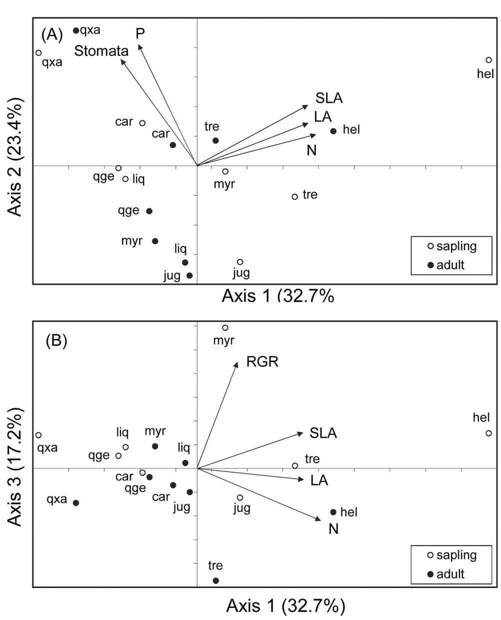

Figure 3. Principal component analysis of saplings and adults of eight tree species in tropical montane cloud forest restoration sites in Veracruz, Mexico. (A) Axes 1 and 2, (B) Axes 1 and 3. Variables are leaf area (LA), specific leaf area (SLA), stomatal density, foliar carbon (C), nitrogen (N), and phosphorous (P), and relative growth rate (RGR). car, *Carpinus tropicalis*; hel, *Heliocarpus donnellsmithii*; jug, *Juglans pyriformis*; liq, *Liquidambar styraciflua*; myr, *Myrsine coriacea*; qge, *Quercus germana*; qxa, *Quercus xalapensis*; tre, *Trema micrantha*.

We found that species with the lowest WD had the highest LA (*H. donnellsmithii*), and intermediate WD species included species with the smallest as well as intermediate LA. The group of species with relatively high WD included the oaks (*Q. germana*, *Q. xalapensis*). As expected, the non-pioneer forest tree species with high WD tend to have low RGR (Jense-ten Klooster *et al.* 2007, Chave *et al.* 2009, Muñiz-Castro *et al.* 2015). Wood density has been reported as being related to leaf size, which decreases with increasing WD (Wright *et al.* 2007). WD tends to be lower in shade intolerant than in shade tolerant species from the same habitat (Lawton 1984, Poorter *et al.* 2008, Chave *et al.* 2009). In temperate forest, both SLA and WD correlated strongly and positively with shade tolerance, and WD negatively with extension growth (Jense-ten Klooster *et al.* 2007). The pioneer species (*H. donnellsmithii*, *T. micrantha*, *M. coriacea*) with high RGR and low-intermediate WD had high SLA and leaf N content. The RGR of these species also changed with age. Adult trees were growing in middle-age plantations where the microenvironmental conditions more closely resemble those of the forest whereas saplings were growing in a more open environment. It has been reported that species with low WD grew fast, were able to respond to periods of higher light availability such as recently established plantations and their growth rates declined as they got bigger (Rüger *et al.* 2012). WD has been negatively correlated with RGR across all plant sizes, as well as during a forest recovery trajectory, and changes in the light and water microenvironmental conditions may explain the switch in growth rates (Gibert *et al.* 2016).

Finally, future research should determine how widespread intraspecific ontogenetic trait variation might be using more focal species across several restoration sites of different age. More important to restoration projects may be deciding which functional traits are relevant to relate interspecific and intraspecific variation to environmental changes during a forest restoration trajectory. One caveat that should be stated here is that this study is based on a limited number of tree species. Clearly, further work is needed to extrapolate any conclusion to other species in other areas. Our results partially supported the initial prediction about differences in traits between saplings and adults of the same tree species because sometimes the ontogenetic difference is fulfilled (*e.g.*, SLA), although not for other traits. Overall, trait variability was higher among species than intraspecifically. Our study suggests that the variation between saplings and adults for most traits is so small that species mean trait values measured in individuals of any age, could be a useful tool to characterize group of species during the forest restoration trajectory, regardless of the ontogenetic variation.

Table 5. Eigenvectors indicating the relative contribution of each of the variables considered in the PCA of the first three principal components (axes 1, 2 and 3). Bold letters indicate a statistically significant contribution ($p < 0.01$) of the variable to the respective eigenvector.

Variable	Axis 1	Axis 2	Axis 3
LA	**0.736**	0.303	-0.079
SLA	**0.716**	0.372	0.253
SD	-0.489	**0.715**	-0.393
C	-0.374	0.114	0.564
N	**0.793**	0.211	-0.369
P	-0.395	**0.867**	0.013
RGR	0.266	0.266	**0.725**

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