

Assessing intraspecific trait variability during seedling establishment to improve restoration of tropical dry forests

OSCAR R. LANUZA,¹ JOSEP M. ESPELTA,² JOSEP PEÑUELAS ^{2,3} AND GUILLE PEGUERO ^{2,3,†}

¹*Facultad Regional Multidisciplinaria Estelí, Universidad Nacional Autónoma de Nicaragua (UNAN Managua/FAREM Estelí), 49, Estelí, Nicaragua*

²*CREAF, Cerdanyola del Vallès 08913 Spain*

³*Global Ecology Unit CREAF-CSIC-UAB, CSIC, Bellaterra 08913 Spain*

Citation: Lanuza, O. R., J. M. Espelta, J. Peñuelas, and G. Peguero. 2020. Assessing intraspecific trait variability during seedling establishment to improve restoration of tropical dry forests. *Ecosphere* 11(2):e03052. 10.1002/ecs2.3052

Abstract. Forest restoration is an effective tool to mitigate climate change, but its implementation in highly diverse and threatened tropical dry forests (TDFs) is particularly challenging due to the hostile environment. Intraspecific trait variability (ITV) in response to these constraints may be very informative for predicting the potential for species acclimation and therefore for improving trait-based species screenings that best match each particular scenario of forest restoration. We analyzed ITV during seedling establishment of three widely distributed and ecologically contrasting TDF species in a greenhouse multifactorial experiment crossing levels of resource availability (nutrients and water) and herbivory to assess the capacity of ITV to discern strategies of seedling establishment and to predict species' growth rates and acclimation potential. The three species studied had contrasting responses to the experimental treatments, suggesting different strategies of seedling establishment. The species with the most plastic pattern of growth performed the best, especially due to its ability to modulate the trade-off of root-to-shoot allocation of biomass depending on nutrient availability. Almost 50% of the variation in the root mass ratio was within species, half of which was a direct response of the treatments, indicating a strong acclimation potential. Individual-level trait measurements, however, were poor predictors of seedling growth rates. ITV, particularly the ability to adapt the pattern of biomass allocation, can be critical during seedling establishment. We propose incorporating information about ITV and the ability of species to modulate their phenotypic expression to cope with environmental variability into programs of forest restoration. Easily implemented and standardized greenhouse experiments are an inexpensive way to obtain high-quality data on the plasticity of forest species, which can be very valuable for predicting the potential of species acclimation and thus improving the selection of species that better match each particular scenario of restoration.

Key words: biomass allocation; forest restoration; functional traits; intraspecific trait variability; plasticity; seedlings; tropical dry forests.

Received 28 November 2019; **accepted** 16 December 2019; **final version received** 14 January 2020. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2020 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** guille.peguero@gmail.com

INTRODUCTION

Avoiding the risks of global warming requires the removal of vast amounts of carbon dioxide from the atmosphere. The Intergovernmental Panel on Climate Change (IPCC) suggests that

one billion more hectares of forest would be needed to limit temperature increases to 1.5°C by 2050 (IPCC [Intergovernmental Panel on Climate Change] 2018). Promoting trees where they can naturally live could account for 90% of this additional area under current climate, so efforts of

forest restoration, including the facilitation of natural regeneration, are among our most effective tools available to mitigate climate change (Chazdon et al. 2016, Bastin et al. 2019, Lewis et al. 2019). To succeed, however, we must overcome several barriers hindering the establishment of tree species, initially by improving species selection to better identify those most adequate to each scenario of forest restoration (Butterfield 1995, Werden et al. 2018).

Nowhere is this need to enhance restoration success more critical than for tropical dry forests (TDF). TDFs remain the most threatened and degraded biome on Earth, with 97% severely endangered due to many anthropogenic pressures (Miles et al. 2006), despite harboring an extremely rich diversity of organisms and a high level of endemism (Banda et al. 2016). Moreover, TDF restoration from degraded woodland and farmland is particularly complex due to the challenging environmental conditions that identify this biome (Vieira and Scariot 2006, Holl 2012, Gei et al. 2018, Werden et al. 2018, Poorter et al. 2019). First and foremost, TDFs typically receive a variable amount of rainfall, between 600 and 1800 mm per year, which is unevenly distributed throughout the year, leading to a pronounced dry season with a high water deficit that can last for 3–6 months (Murphy and Lugo 1986, Gillespie et al. 2000). The high seasonality of precipitation strongly influences plant phenological patterns such as seedling establishment, which must occur during the limited opportunity represented by the wet season (Lieberman 1982, Lieberman and Li 1992, Ceccon and Hernández 2009). Seedling survival in TDFS is strongly limited by water availability (Murphy and Lugo 1986, Vieira and Scariot 2006, Werden et al. 2018), despite the high levels of germination from soil seed banks during the favorable season (Lieberman and Li 1992, Ceccon et al. 2004). Converting TDFs into agricultural land is also typically followed by the rapid depletion of stocks of available soil nutrients (Kauffman et al. 1993), and this irreversible loss of fertility constrains the natural regeneration of secondary forests (Campo and Vázquez-Yanes 2004), particularly in low-resource environments such as TDFs (Poorter et al. 2019). Finally, pressure from both wild and increasing numbers of domestic herbivores adds another burden that

reduces success rates during the transition from seedling to sapling (Holl and Quiros-Nietzen 1999).

The competition for below- and aboveground resources is strong during seedling establishment, and obtaining sufficient supplies of water, nutrients, and light becomes vital for sustaining an adequate rate of growth (McMurtrie et al. 2008, Ågren et al. 2012, Poorter et al. 2012, Faticchi et al. 2014). Plants can adapt their pattern of biomass allocation as a function of the external environmental conditions (Johnson and Thornley 1987, Gedroc et al. 1996, Poorter et al. 2012, Faticchi et al. 2014). The classical functional equilibrium hypothesis predicts that plants under a given stress maximize their surface area to acquire the most limiting resource (Brouwer 1963). Plants consequently allocate more biomass to roots when water and nutrients are the most limiting factors and promote stem and foliar mass when light is lacking or to compensate for losses from defoliation due to herbivory (Chapin et al. 1987, Tilman 1988, Gedroc et al. 1996, Poorter et al. 2012, Ledo et al. 2018). This phenotypic plasticity, that is, the ability of a genotype to modulate the expression of its functional traits in response to environmental conditions, may be highly adaptive for seedling acclimation during their establishment at a given microsite (Bradshaw 2006, Valladares et al. 2007). Additionally, plant traits must be functional and therefore affect individual survival, growth, and/or reproduction, a central tenet of trait-based ecology (Paine et al. 2015, Poorter et al. 2018, Yang et al. 2018). Hence, a high intraspecific trait variability (ITV) at an individual level could be a better predictor of plant growth than species-level averages (Poorter et al. 2018).

Screening tree species based on their functional traits may improve the success of seedling establishment in harsh ecosystems such as TDFS (Werden et al. 2018). Including ITV measurements of easily measured traits for selecting species may therefore be a logical extension. The classical view that biomass allocation must be functional and thus responsive to the environment has nevertheless been contested (Poorter and Nagel 2000, Reich 2002), and the relationships between ITV and demographic rates (e.g., growth, survival, and reproduction) still remain unclear (Poorter et al. 2018, Yang et al. 2018).

The integration of ITV and plasticity in programs of forest restoration may thus remain rare, although it can provide valuable qualitative information on species performance (Valladares and Gianoli 2007). For example, a recent large-scale assessment of successional dynamics identified N-fixers as disproportionately successful in TDFs (Gei et al. 2018). However, coexisting tree species within the legume family have different ecological strategies linked to disparate functional traits, including seed and foliar size or the level of protection against herbivores, all of which can be key features during seedling establishment but almost nothing is known about how plastic they are. Furthermore, rapidly growing species can have an advantage only if associated with a flexible pattern of resource allocation that can modulate growth to match local resource conditions, but this strategy could in turn be disadvantageous if it does not have a trade-off with protection against herbivores.

In order to fill this gap, we studied the intraspecific variability of patterns of biomass allocation and functional traits during the establishment of seedlings of three widely distributed TDF tree species (*Guazuma ulmifolia* Lam. Malvaceae; *Enterolobium cyclocarpum* Griseb. and *Vachellia pennatula* Seigler & Ebinger. both Leguminosae; hereafter *Guazuma*, *Enterolobium*, and *Vachellia*, respectively) growing under contrasting scenarios of resource availability (nutrients and water) and herbivory levels. *Guazuma* is a small tree with tiny seeds and no physical protection against herbivory. *Enterolobium* and *Vachellia* are both N-fixers with bipinnate leaves and abundant woody spines but contrasting seed, foliar, and adult sizes. These three species are representatives of the ecological strategies during the early to mature stages of forest succession in TDFs (Esquivel et al. 2008, Lebrija-Trejos et al. 2010). We accounted for ontogenetic effects by measuring height; total dry biomass; mass ratios of roots, stems, and leaves; dry-matter content; leaf area ratio (LAR, total area of leaves of a seedling divided by its total dry mass in cm^2/g); and specific leaf area (SLA, the area of leaves per unit dry mass in cm^2/g) 60 d after germination (i.e., the pretreatment acclimation period) and 45 and 90 d after the onset of the experimental treatments. We hypothesized that (1) seedlings would adapt the phenotypic expression of their

functional traits in response to resource availability and herbivore pressure in order to maximize their growth rates, (2) the species with the most variable intraspecific functional traits and the most flexible pattern of biomass allocation would have the higher growth rates and achieve the greatest biomass on average across all experimental scenarios, and (3) traits with higher intraspecific variability would better account for seedling responses to the experimental treatments and ultimately would be better predictors of the changes in species' growth during seedling establishment when measured at an individual level.

MATERIALS AND METHODS

Study site

This study was carried out in the greenhouse of the El Limón Experimental Station (13°03'44" N, 86°21'57" W), which is managed by the Regional Multidisciplinary Faculty of Estelí (National Autonomous University of Nicaragua—Managua). This research facility is at 888 m a.s.l. in northwestern Nicaragua and has a dry tropical climate typical of the region, with temperature ranging from 16° to 33°C and a mean annual precipitation of 830 L m^{-2} , 90% of which falls during a 6-month wet season that usually lasts from May to November (Peguero et al. 2012).

Species, seed collection, and seedling production

We selected *G. ulmifolia*, *E. cyclocarpum*, and *V. pennatula* because they are representatives of the ecological strategies during the early to mature stages of forest succession in TDFs (Esquivel et al. 2008, Lebrija-Trejos et al. 2010). All three species are native, abundant, and widely distributed from Mexico to South America, from lowland to montane forests up to 1400 m a.s.l., and are therefore of interest for programs of forest restoration (Stevens et al. 2001, Barrance et al. 2003). *Guazuma* is a small tree with tiny seeds (0.004–0.01 g per seed) and no physical protection against herbivory, but *Enterolobium* and *Vachellia* are both N-fixers with bipinnate leaves and copious woody spines but with contrasting sizes of seeds (0.83–1.11 vs. 0.06–0.1 g per seed), leaves (0.93 vs. 0.18 cm leaflet length), and adults (30 vs. 8 m average height). All have hard physically dormant seeds usually dispersed by

endozoochory by large domestic or wild animals (Peguero et al. 2012, Peguero and Espelta 2013). The seeds for this study were collected from at least four mature trees per species at the El Limón research station, thus covering the natural genetic variability of the local population of the three species. Following previous studies (Peguero et al. 2012, Peguero and Espelta 2013), we mechanically scarified seeds of *Vachellia* and *Enterolobium* to break down the testa allowing the endosperm to absorb water and trigger germination; *Guazuma* seeds were soaked in water at 80°C for three minutes, then in water at ambient temperature for 24 h more, and finally gently cleaned the characteristic protective mucilage of the seeds. All seeds were then placed in Petri dishes with adsorbent paper and kept wet until the emergence of the hypocotyl, when they were sown in plastic trays containing a growth substrate medium (PRO-MIX, Premier Tech, Rivière-du-loup, Quebec, Canada). Seedlings with their first pair of true leaves were transplanted into polyethylene bags filled with a local superficial Cambisol and were acclimated to the greenhouse conditions for 60 d.

Experimental design and data collection

We designed a multifactorial experiment with two levels of nutrient and water availability and two levels of simulated herbivory (i.e., three fully crossed two-level factors for $2 \times 2 \times 2 = 8$ combinations of experimental treatment). The nutrient addition was a single initial application of one gram per bag of an all-purpose 15-15-15 NPK fertilizer (treatment and control hereafter denoted as N+ and N-, respectively). The field capacity of the soil was determined, and the water treatment was then based on the weekly watering of the seedlings at full or half field capacity (hereafter denoted as W+ vs. W-, respectively). The simulated herbivory consisted in the removal of 50% of the leaves of each seedling. This treatment was applied twice, first after the 60-d acclimation period and then 45 d after the onset of the experimental treatments (intermediate stage). We had a sample size of 20 seedlings per species and treatment combination. All seedlings grew under the same light conditions inside the greenhouse. After a 60-d acclimation period and prior to applying the treatments, we measured plant height (in cm) and weighed the

fresh masses of the roots, stems, and leaves and then the dry mass of each fraction on an additional 20 seedlings after oven-drying in separate paper envelopes at 80°C for 24 h (hereafter referred as root, stem, and leaf mass ratios, RMR, SMR, and LMR, respectively, in g/g dry weight), thus also obtaining the dry-matter content (DMC, %). Each fresh leaf was then scanned, and its area determined, using ImageJ (Schneider et al. 2012) to obtain LAR and SLA (Poorter et al. 2012, Pérez-Harguindeguy et al. 2013). We again measured the same traits in the corresponding set of seedlings 45 and 90 d after the onset of the experimental treatments (i.e., at the intermediate and final stages).

Data analyses

We assessed the differences between the species before the application of the experimental treatments by calculating a plasticity index (i.e., the highest value of a trait along the range of an environmental factor considered divided by the lowest value, Poorter et al. 2012) for each of the traits measured and building general linear models to evaluate the among-species variation after the acclimation period both for the traits and for their plasticity metrics. We then identified the main axes of covariation of the traits within and between species in a multivariate space using a principal component analysis (PCA). We also evaluated the amount of this trait variation between versus within species and also within species due to the experimental treatments by a variance component analysis using nested linear mixed-effects models. Briefly, this procedure consists of fitting separate linear mixed-effects models for each trait, first with species as the only random factor, thus obtaining the amount of variance explained within and between species, and then with treatment nested within species as random factors, therefore also obtaining the amount of within-species variance due solely to the application of the experimental treatments (Vilà-Cabrera et al. 2015 for further details on the method). Finally, we calculated trait hypervolumes based on the pattern of allocation of biomass into leaves, stems, and roots to visualize the functional niche of each species, their overlap and similarity, and their changes during seedling development (ontogeny). We used the hypervolume R package that can construct n-dimensional

hypervolumes by estimating Gaussian kernel density on an adaptive grid of random points around the empirical observations (see Blonder et al. 2014 for further details of this methodology). We selected LMR, SMR, and RMR for the variance component analysis and the construction of the functional hypervolumes because their large and nearly orthogonal loading in the initial PCA identified them as the best traits to synthesize differences between species of their strategy for seedling establishment (Fig. 1).

We evaluated the initial species differences and the potential plasticity of each trait and then analyzed the responses of the seedlings to the experimental treatments using a series of linear models. We first analyzed seedling total dry mass (TDM) produced and then determined its variation in the expression of some key functional traits: DMC, LMR, SMR, and RMR. These traits were selected for their potential to account for the differences between species in seedling growth strategy based on their loadings and lack of covariation in a final PCA (Fig. 1). We also used linear models to examine shifts in the trade-off between above- and belowground compartments due to the experimental treatments. The best linear models were chosen by automated model selection based on the dredge function of the MuMIn R program (Bartoń 2019). This method of model selection generally consists in first building a saturated model containing all experimental factors, that is, species, time, nutrients, water, and herbivory, and all possible second-order interactions between them. All possible combinations are then automatically run and ranked by their second-order Akaike information criterion (AIC_c). All models with $\Delta AIC_c < 2$ were considered to have analogous goodness of fits and therefore outputs and explanatory powers, and residual diagnostic plots were individually assessed to identify significant effects and check model performance. Differences between groups were determined using Tukey post hoc tests based on marginal means estimated from each linear model with the emmeans R package (Lenth 2019).

Finally, we ranked each trait by its coefficient of variation at the end of the experiment and then assessed its explanatory power for the rate of seedling growth using equivalent linear models, with species as a fixed factor and each trait as a

single covariate. We specifically compared the predictive ability of the models in these analyses, depending on whether the traits were measured at an individual level, thus introducing ITV, or alternatively conflating predictive ability into species using treatment means. We also used a similar automated model selection to identify the trait combination that best predicted seedling growth rate, again with species as a fixed factor but also including all measured traits and their second-order interactions as covariates. All statistical analyses used R version 3.5.1 (R Core Team 2019).

RESULTS

Initial patterns of seedling growth

The seedlings of the three species differed greatly in height, TDM, LMR, SMR, RMR, and LAR after the 60-d acclimation period, although they had similar SLAs (Table 1). Young *Guazuma* seedlings, developed from smaller seeds, were shorter and had a lower TDM, but their relative investment in acquisitional tissues (e.g., LMR and LAR) was significantly larger than for *Vachellia* and *Enterolobium* seedlings of the same age. *Guazuma* also had higher plasticity indices (e.g., height, TDM, RMR, SMR, and LAR), generally followed by *Vachellia*, and *Enterolobium* seedlings generally had a more rigid growth strategy and narrower trait expression. A PCA of all traits indicated that the first two axes represented >75% of the total trait variability after the acclimation period, and the spread within this multivariate space was smaller for *Enterolobium* than *Guazuma* and *Vachellia* seedlings (Fig. 1a). The patterns of biomass allocation between above- and belowground structures clearly segregated the three species, and the vectors of LMR, SMR, and RMR were nearly orthogonal, thus identifying these traits as good descriptors of the early growth strategies of the seedlings.

Variation in biomass allocation

The partitioning of trait variance indicated that most of the variability in the allocation patterns was due to differences across species (Fig. 2). Species-level differences at the end of the acclimation period accounted for 60–80% of the total variation in biomass allocated to roots, stems, and leaves. The intraspecific component as seedlings developed over time nonetheless increased

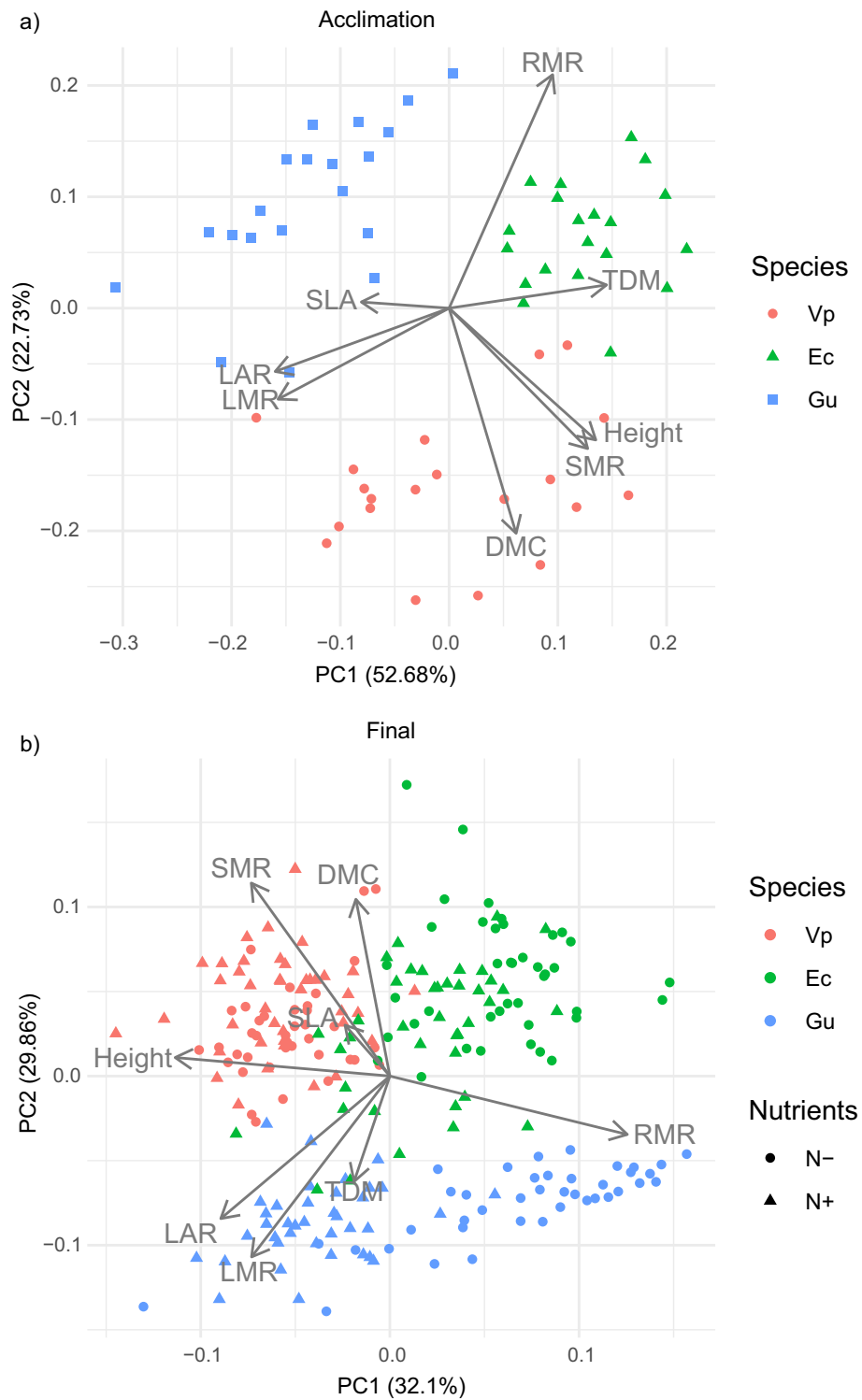


Fig. 1. Principal component analyses of multivariate-trait associations of seedlings of *Guazuma ulmifolia* (Gu), *Enterolobium cyclocarpum* (Ec), and *Vachellia pennatula* (Vp): (a) after 60 d of acclimation to greenhouse conditions and (b) at the end of the experiment (final). See Table 1 for trait abbreviations and descriptions.

Table 1. Initial among-species differences in functional traits of seedlings after the acclimation period.

Trait	<i>Vachellia pennatula</i>		<i>Enterolobium cyclocarpum</i>		<i>Guazuma ulmifolia</i>	
	Mean \pm SE	PI	Mean \pm SE	PI	Mean \pm SE	PI
Height (cm)	31.9 \pm 1.8 ^a	3.48	32.1 \pm 2.6 ^a	1.92	9.7 \pm 2.6 ^b	4.17
DMC (%)	50.0 \pm 0.1 ^a	1.71	32.6 \pm 0.1 ^b	1.89	25.2 \pm 0.1 ^c	1.7
RMR (g/g)	0.2 \pm 0.02 ^c	3.65	0.465 \pm 0.02 ^a	1.7	0.345 \pm 0.02 ^b	5.59
SMR (g/g)	0.3 \pm 0.01 ^b	2.21	0.342 \pm 0.02 ^a	1.63	0.131 \pm 0.02 ^c	3.56
LMR (g/g)	0.5 \pm 0.02 ^b	2.2	0.19 \pm 0.02 ^c	4.64	0.52 \pm 0.02 ^a	2.03
LAR (cm ² /g)	167.8 \pm 12.4 ^b	3.59	73.21 \pm 17.5 ^c	9.95	212.8 \pm 17.5 ^a	3.8
SLA (cm ² /g)	361.9 \pm 18.6	3.27	369.79 \pm 26.36	2.62	398.77 \pm 26.4	2.04

Notes: Mean \pm standard error (SE) and plasticity index (PI, Poorter et al. (2012)) of total dry mass (TDM); dry-matter content (DMC); root, stem, and leaf mass ratios (RMR, SMR, and LMR, respectively); leaf area ratio (LAR); and specific leaf area (SLA) after 60 d of acclimation to controlled greenhouse conditions ($n = 20$ individuals per species). Different letters within a row denote significant differences among species based on a Tukey HSD post hoc test.

due to ontogenetic drift (i.e., the constitutive component of ITV) but also due to within-species variations arising from the different experimental treatments, which changed the environmental conditions where each seedling had grown. The amount of resources allocated to roots was particularly responsive and was the most plastic

attribute. The differences between species by the end of the experiment only explained half of the total RMR variability, and within-species and treatment-associated variability each accounted for 25%, so the seedlings clearly adjusted their relative investment in root development to the growing conditions.

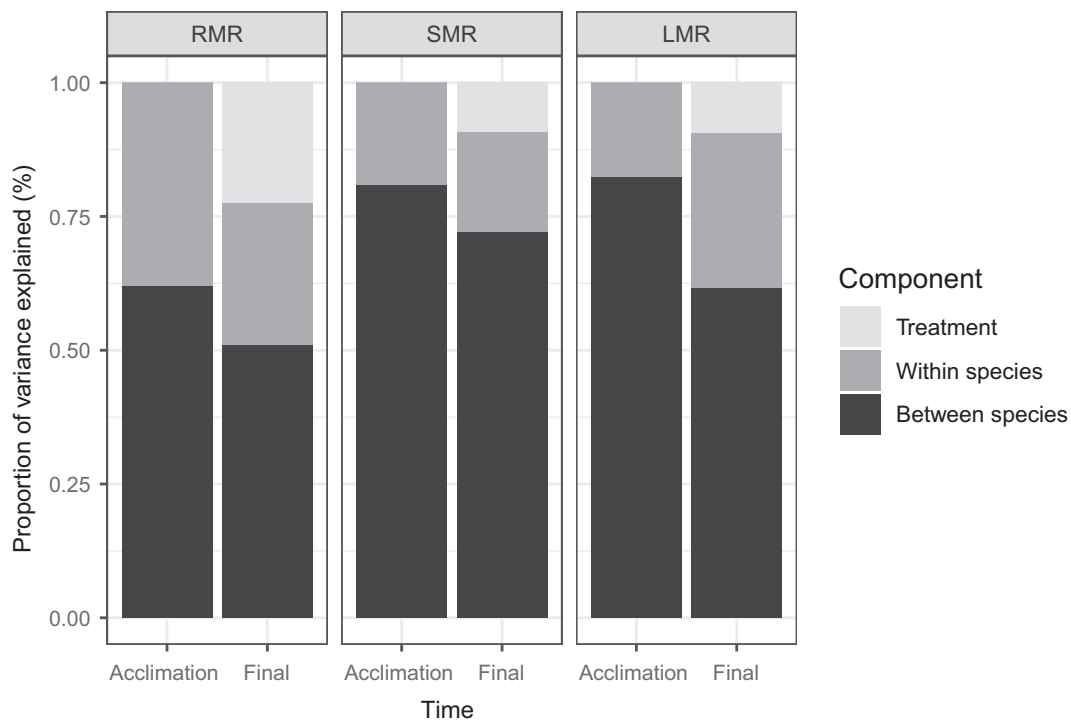


Fig. 2. Proportions of variance in root, stem, and leaf mass ratios (RMR, SMR, and LMR, respectively) explained by differences between species (black), by differences between individuals within species (dark gray), and by the effect of the experimental treatments (light gray) at the end of the pretreatment stage (acclimation) and at the end of the experiment (final). Sample sizes are 20 and 160 seedlings per species for the acclimation and final periods, respectively.

The reconstruction of the functional hypervolumes identified species-specific differences in allocation patterns. *Guazuma* and especially *Enterolobium* seedlings increased their hypervolumes over time, but the space occupied by the *Vachellia* seedlings decreased by the end of the experiment (Table 2, Fig. 3). Both the *Enterolobium* and *Guazuma* seedlings nearly filled the entire range of RMR and LMR by the end of the experiment, although the *Guazuma* seedlings had less of an overlap of the hypervolume between the acclimation and the final period, indicating a shift in its pattern of biomass allocation during seedling development.

Effects of the treatments on seedlings and growth trade-offs

The *Guazuma* seedlings had higher growth rates and thus attained larger intermediate and final biomasses, even though they showed the smallest size after the acclimation period (species \times time in TDM, $F_{2, 462} = 11.2$, $P < 0.001$; Fig. 4a). The *Guazuma* seedlings were likewise the most responsive to nutrient level and grew more when they received extra fertilization (species \times nutrients in TDM, $F_{2, 462} = 6.9$, $P < 0.01$; Fig. 4b) or when they allocated more resources to root development when nutrient availability was lower (species \times nutrients in RMR, $F_{2, 462} = 41.7$, $P < 0.0001$; Fig. 4d). The *Vachellia* seedlings were more lignified and were able to compensate for losses after the experimental defoliation by a rapid additional foliar flushing that reduced their generally higher

DMC (species \times herbivory in DMC, $F_{2, 462} = 10.7$, $P < 0.001$; Fig. 4c). In contrast, the *Guazuma* seedlings had the lowest DMC, most likely due to their shorter stems, but their growth patterns corresponded with the level of nutrients in their establishment site (species \times nutrients in SMR, $F_{2, 462} = 20.1$, $P < 0.0001$; Fig. 4e; and in LMR, $F_{2, 462} = 23.7$, $P < 0.0001$; Fig. 4f). Above- and belowground structures had a strong trade-off in biomass allocation: The larger the amount of resources invested in roots, the lower the mass of leaves (Fig. 5). The *Guazuma* seedlings invested significantly fewer resources in roots and therefore more in leaves when grown at higher nutrient levels, despite the generally negative relationship between leaves and roots, and the *Vachellia* and *Enterolobium* seedlings did not shift their patterns of biomass allocation (Fig. 1b and marginal density plots in Fig. 5, species \times nutrients interaction in the relationship between RMR and LMR, $F_{2, 468} = 10.2$, $P < 0.0001$, see Table S1 for a complete model summary).

Finally, both RMR and LMR had high levels of variation by the end of the experiment, particularly at the intraspecific level, due to the effects of the treatments (Figs. 1b, 6a). Including this ITV for individual measurements, however, did not improve the explanatory power of RMR and LMR for seedling growth rate (Fig. 6b). Species \times treatment averages always outperformed individual-level data, except for DMC and SLA. The automated model selection of the best combination of traits for predicting growth rates produced five models with statistically equivalent

Table 2. Hypervolumes of the trait spaces for biomass allocation occupied by each species and their similarity after the acclimation period and at the end of the experiment.

Hypervolume similarity								
	Species	Total hypervolume	Acclimation			Final		
			<i>Gu</i>	<i>Vp</i>	<i>Ec</i>	<i>Gu</i>	<i>Vp</i>	<i>Ec</i>
Acclimation	<i>Gu</i>	0.030	1	0.165	0	0.074	–	–
	<i>Vp</i>	0.036		1	0.08	–	0.038	–
	<i>Ec</i>	0.010			1	–	–	0.203
Final	<i>Gu</i>	0.041				1	0.069	0.122
	<i>Vp</i>	0.012					1	0.185
	<i>Ec</i>	0.040						1

Notes: Functional hypervolumes of seedlings are based on the patterns of biomass allocation and were built by estimating Gaussian kernel density (unitless 3D volumes, see text for further details). *Gu*, *Vp*, and *Ec* denote *Guazuma ulmifolia*, *Vachellia pennatula*, and *Enterolobium cyclocarpum*, respectively. Similarities of the hypervolumes are Jaccard indices compared between species within the same study period and within species between experimental periods (pre- versus post-treatment). Note that 1 denotes total overlap and similarity of the trait space occupied.

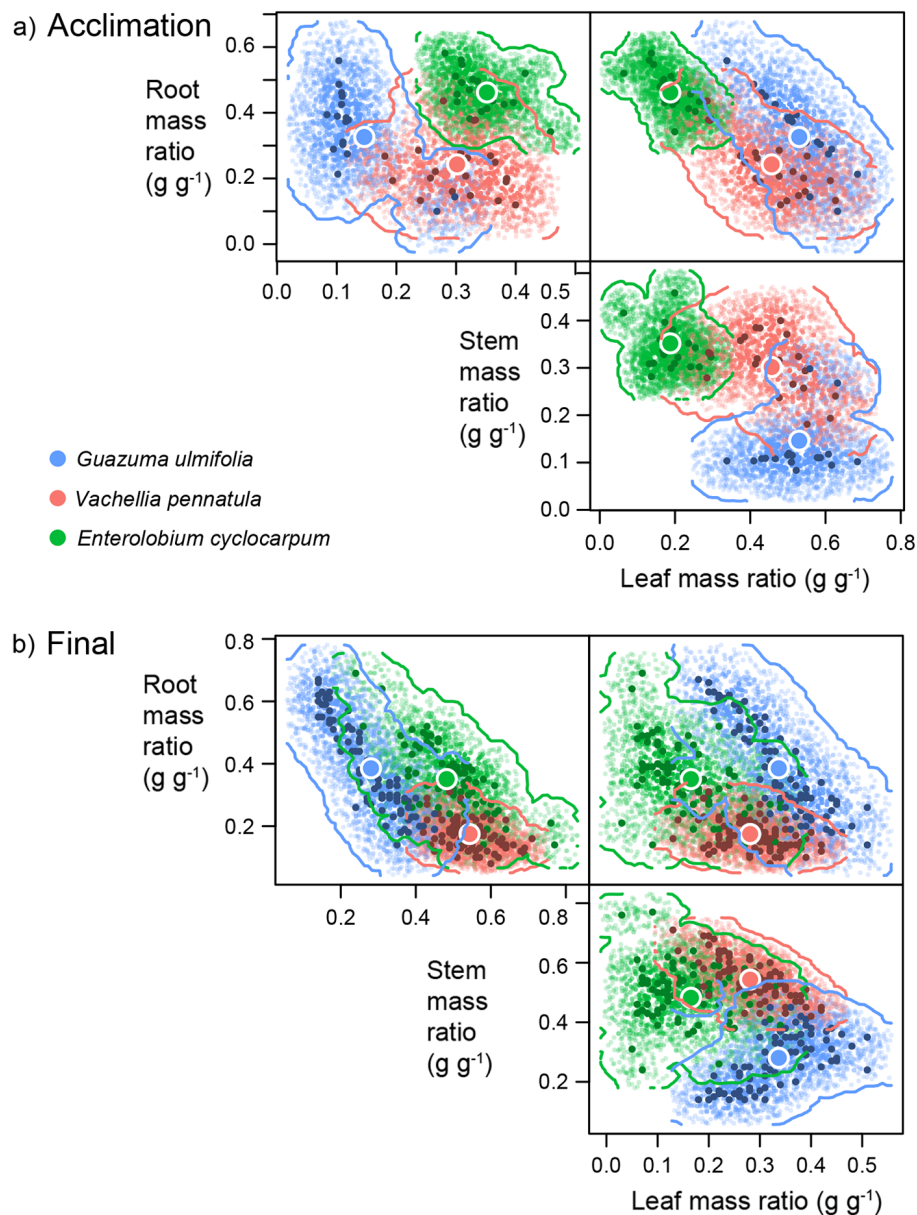


Fig. 3. Hypervolumes of the trait spaces for biomass allocation occupied by species: (a) after the acclimation period and (b) at the end of the experiment.

fits (difference in $\text{AIC}_c < 1$). Individually measured height, DMC, RMR, and LMR in all these most parsimonious models were always included and together explained 50% of the variation in growth rate. Height and RMR were positively and negatively correlated with growth rates, respectively, regardless of the individual or species level of the data (Appendix S1: Fig. S1).

In contrast, seedling DMC was only correlated with growth rate when measured individually.

DISCUSSION

We assessed the ability of three TDF tree species to modulate their expression of functional traits and pattern of biomass allocation during

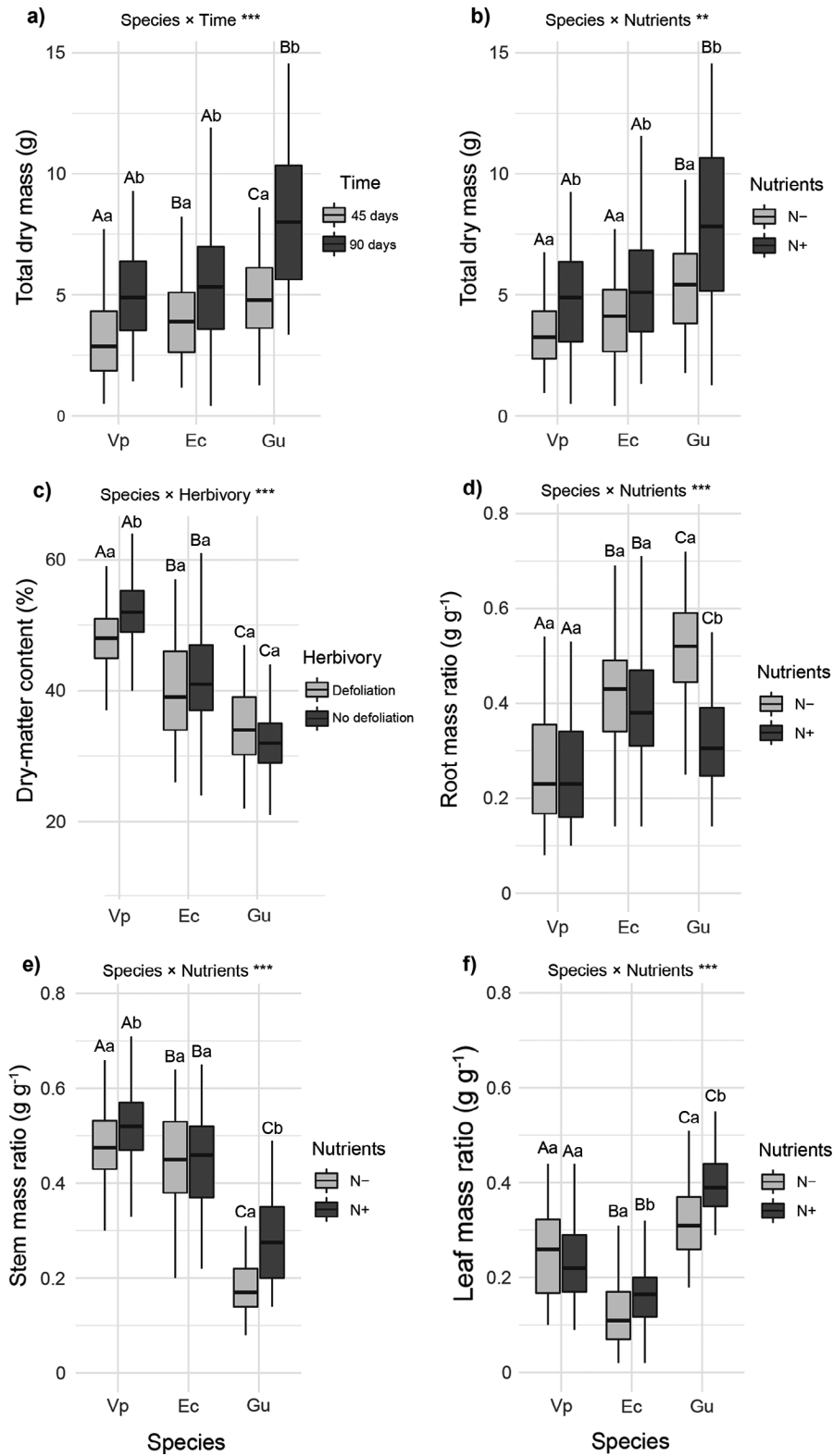


Fig. 4. Responses of the seedlings of *Guazuma ulmifolia* (Gu), *Enterolobium cyclocarpum* (Ec), and *Vachellia*

(Fig. 4. Continued)

pennatula (Vp) to the experimental treatments: (a) total dry mass produced over time (45 and 90 d after the application of the treatments), (b) depending on nutrient availability (N– and N+ are lower and higher nutrient availability, respectively), (c) proportion of dry-matter content in response to simulated herbivory and change in the ratio of biomass allocated to roots (d), stems (e), and leaves (f) depending on nutrient availability. ** and *** denote significant differences ($P < 0.01$ and $P < 0.001$, respectively) of the corresponding interactions based on linear models. Different upper- and lowercase letters denote significant differences ($P < 0.05$) between species within the same treatment and within species between treatments, respectively, based on Tukey's post hoc tests with marginal means estimated from the corresponding linear model.

seedling establishment in response to environmental variation and used this information to improve our ability to predict their growth performance. Biomass allocation, the changes of the functional hypervolume over time, and the sensitivity to modulate the growth pattern

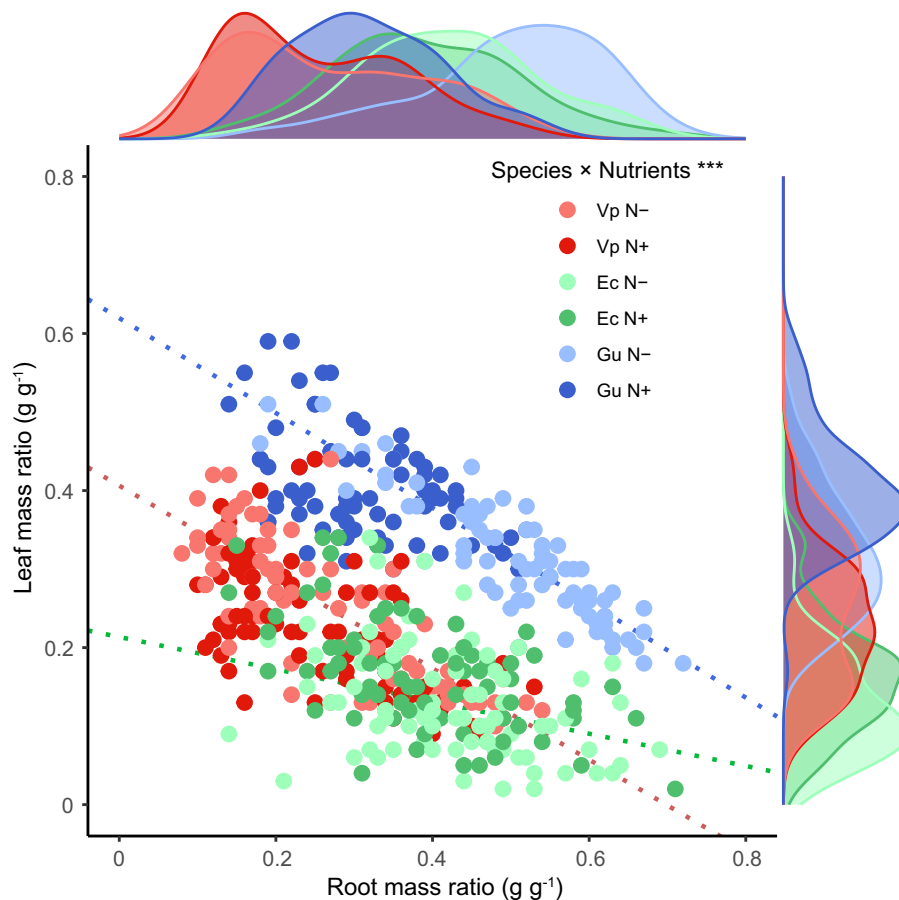


Fig. 5. Differences in the trade-off between the amount of biomass allocated to leaves or roots for the seedlings of *Guazuma ulmifolia* (Gu), *Enterolobium cyclocarpum* (Ec), and *Vachellia pennatula* (Vp). Marginal density plots show the among-species variation in root and leaf mass ratios depending on the level of nutrient availability (N– and N+ for lower and higher nutrient availability, respectively; see color legend in the inset). *** denotes a significant difference ($P < 0.0001$) for the interaction between species and nutrient treatment based on a linear model. See Appendix S1: Table S1 for the complete model output.

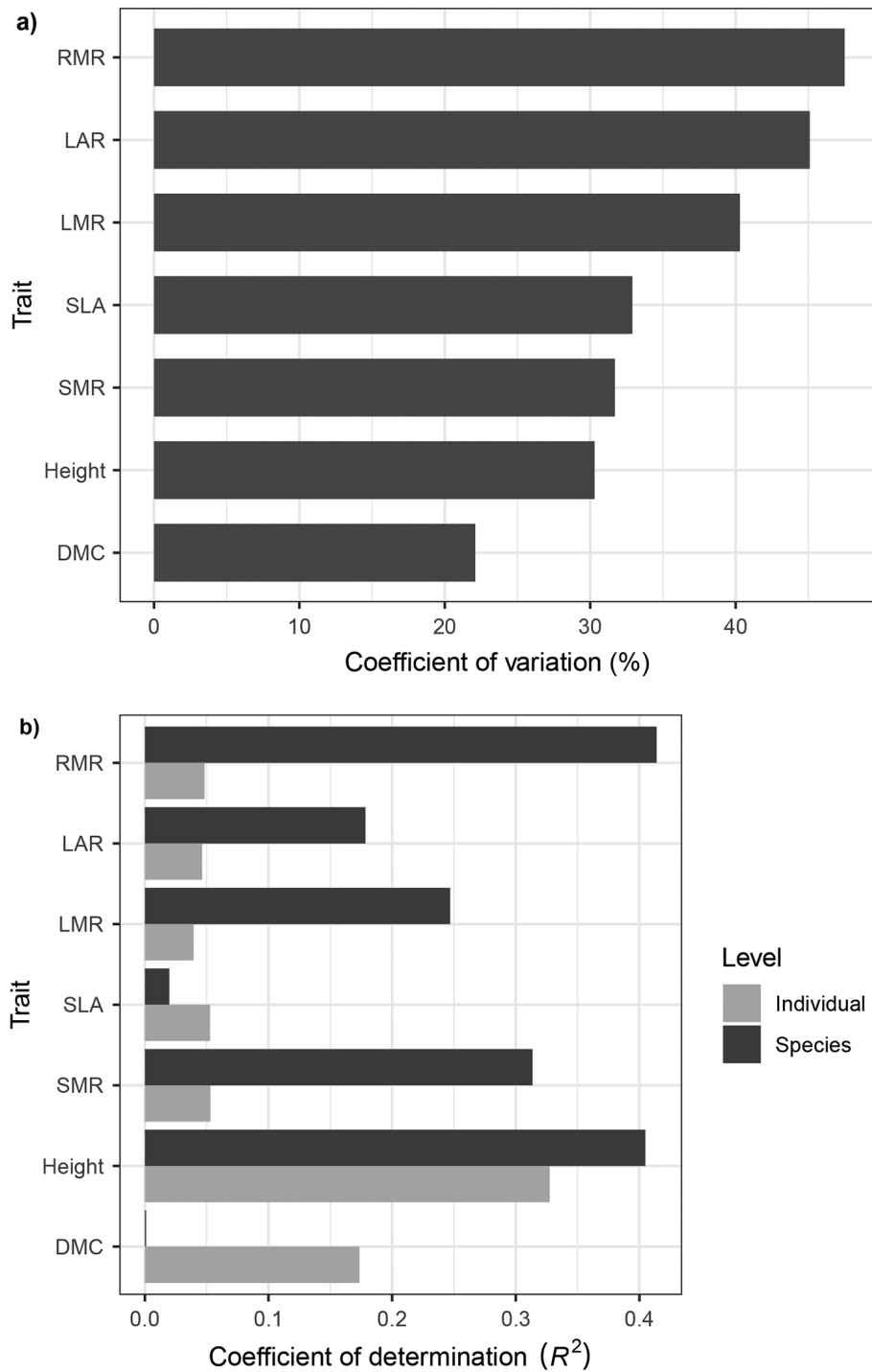


Fig. 6. Variability and explanatory power of seedling traits for the growth rates: (a) coefficients of variation at the end of the experiment and (b) coefficients of determination (R^2) of each trait as a covariate based on linear models at the individual level (gray bars) and the species level based on mean trait values per species by experimental treatment (black bars).

following the experimental treatments differed among the three species, highlighting key differences in the strategies of seedling establishment. Between 40% and 50% of the variation in the balance of biomass allocation to roots and leaves was due to intraspecific variability, indicating a strong potential for adjustment to local environmental conditions (Poorter et al. 2018). *Guazuma* was best able to fine-tune this trade-off with the environment of each particular establishment site and attained a larger biomass in most of the experimental conditions. Single traits such as height, RMR, or LMR were the best predictors of the rate of seedling growth. Their predictive power, however, was surprisingly lower when measured at an individual level than when averaged per species and experimental treatment.

The capacity to regulate the pattern of biomass allocation as a function of abiotic and biotic constraints is highly adaptive and plays a critical role in the success of the transition from seedling to sapling (Brouwer 1963, Lloret et al. 1999, Markesteijn and Poorter 2009). Our results indicated that the expression of the trade-off between below- and aboveground structures retained a high level of intraspecific variability and was sensitive to the varying experimental conditions. Nearly 50% of the variation in the amount of resources invested in root construction was due to within-species variability, and nearly half of this variation was a direct response to the experimental treatments. In contrast to previous assessments (Markesteijn and Poorter 2009, Poorter et al. 2012, Ledo et al. 2018), the driving role of water supply in our experiment was minor compared to nutrient availability, perhaps due to the moderate watering treatment, because irrigating at half of the soil carrying capacity on a weekly basis inside a greenhouse likely differs greatly from the actual water shortage experienced by seedlings in natural TDF conditions (Werden et al. 2018). The species with the most adaptable pattern of root-to-shoot allocation and a greater responsiveness to nutrient levels attained the highest biomass and growth rate in most of the conditions. Seedling survival during the unfavorable dry season is usually positively correlated with root allocation in nutrient- and water-limited ecosystems (Lloret et al. 1999, Werden et al. 2018). An adequate nutrient supply also allows

the seedlings of tropical trees to reduce their fine-root biomass while improving their photosynthetic rates and capacity to transport water (Wright et al. 2011, Santiago 2015). Our results, however, also highlight the contrast among species in their ability to adjust their growth to the variable environmental conditions present at each establishment site, particularly to variations in nutrient availability, and so indicate the differences in their capacity to take advantage of local environmental features (Santiago 2015). These findings support the long-standing view, although sometimes contested (Reich 2002), that the allocation of seedling biomass is fully functional (Brouwer 1963, Markesteijn and Poorter 2009, Poorter et al. 2012) and also suggest that intraspecific variability or even the adaptive plasticity of functional traits, particularly of allocation trade-offs, may help TDF seedlings to acclimate to microsite conditions and therefore increase their probability of establishment.

The three species in this study are widely distributed representatives of TDFs from Mesoamerica and are common in secondary forests and as early pioneers in abandoned pastures (Stevens et al. 2001, Barrance et al. 2003). They have, however, contrasting and ecologically relevant features that represent key differences in their strategies of seedling establishment. Our measurements immediately after the acclimation period, that is, before the onset of the experimental treatments, identified large differences in mean trait values between species and in the plasticity of their expression. Some of these initial variations can be partly determined by the large among-species differences in seed size, where nutrient reserves are crucial during early seedling development (Kitajima and Fenner 2000). The seedlings of the two caesalpinoid legumes accordingly grew higher after the acclimation period, but their investment in root and foliar development differed in their regeneration niches, even though both are N-fixers and have bipinnate leaves. Bipinnate leaves and the ability to fix N are advantageous traits for coping with the low N availability and the high irradiance and foliar temperature that typically compromise the gain of carbon in secondary TDFs (Gei et al. 2018). Biomass allocation, however, was more flexible for the *Enterolobium* than the *Vachellia* seedlings, whose functional hypervolume

actually decreased over time, indicating a very constrained growth pattern. In contrast, the greater lignification of the *Vachellia* seedlings and their ability to quickly compensate defoliation suggest that this species is better equipped to cope with herbivory, consistent with its spinescence and strong ability to resprout that allow it to easily colonize pastures (Peguero and Espelta 2011). Even closely related species may have contrasting strategies of establishment and could therefore serve different purposes in TDF restoration, depending on the specificities of the local conditions.

We also addressed the relationship between ITV and seedling performance, testing the hypothesis that trait measurements at an individual level should be better predictors of growth rates than species means and that more variable traits should outperform traits whose phenotypic expression is more constrained. In all our studied traits (except DMC and SLA), species \times treatment means were better predictors of seedling growth than individual measures. Our models with individual-level trait data explained 4–5% of the variation in growth. This unexpected result is similar to the 3.1% reported by a recent global-scale effort to link functional traits with plant growth rates (Paine et al. 2015). Some recent attempts to explain this paradox suggest several methodological, conceptual, and ecological issues (Poorter et al. 2018, Yang et al. 2018). From a methodological point of view, accurately recording growth and some soft (i.e., easily measured) traits is not as straightforward as usually assumed, so measurement errors may lead to weak trait–growth relationships (Poorter et al. 2018). This problem should mainly affect field studies, where growth rates are derived from nondestructive measures of whole-plant biomass such as increases in stem diameter, but we cannot presume that our study was free of measurement error. Moreover, our understanding of trait–network relationships is still poor, and the observed covariation of multiple traits indicates the need to incorporate the whole phenotypic context as seems unreasonable to expect a single trait to predict demographic rates such as growth, reproduction, or survival (Yang et al. 2018). A given trait may be crucial for a particular demographic component and also have a restricted phenotypic expression around a

species-specific mean that warrants this functional linkage. If so, any individual plant would have to modulate the expression of other indirectly related traits to secure this relationship, so no association could be detected between environment and demographic rates with this hypothetical key although rigid functional trait. Finally, from an ecological perspective, the phylogenetically limited scope of our study may restrict the variation of growth rates and functional traits that prevent finding stronger associations (Poorter et al. 2018). Extending this kind of standardized manipulative experiment, both in controlled and field conditions, to more tree species covering the entire spectrum of plant traits as much as possible should allow us to appropriately test the extent to which ITV is truly adaptive, or alternatively the consequence of ontogenetic drift, tissue aging, or even an evolutionary by-product within the reaction norm of the genes that control the plastic expression of the so-called functional traits (Via 1993).

Height in our experiment also had substantial explanatory power for seedling growth rates, irrespective of the level of the data used, supporting the adaptive (or maladaptive) view and consistent with the results reported by Poorter et al. (2018). The direct relationship between height and the size of each plant compartment, and thus of photosynthetic and nutrient-acquiring tissue, has been recognized previously, and it is perhaps the best integrative measure of overall seedling performance (Poorter et al. 2018). Seedling height after 90 d in an experimentally variable environment cannot be considered a functional trait *sensu stricto* but is both informative and useful from an applied perspective, because it is clearly correlated with the ability of each species to grow. Focusing just on height, however, may overlook other important features of the establishment strategy of tree species since it may not capture the outcome in the above- and below-ground trade-off due to contrasting resource availability. Likewise, a trait such as SLA that is central in the current paradigm of the global spectrum of plant traits (Díaz et al. 2016) was particularly poorly correlated with growth, even when averaging ITV with species by treatment means, again consistent with previous studies in tropical forests (Poorter et al. 2018, Werden et al. 2018). Variable and responsive traits such as

RMR and LMR were nevertheless relatively good predictors of seedling growth, as expected, particularly when averaged with species by treatment, suggesting that some traits represented the variability among species in their capacity to modulate biomass allocation to cope with environmental variability.

Screening of species based on their functional traits will be crucial for restoring TDF to their original state (Werden et al. 2018). To succeed, however, functional traits must be incorporated not only as species averages but also taking into account their variation within species and even the species' ability to modulate their phenotypic expression to cope with environmental variability. ITV does not substantially improve our predictive ability of species growth rates in variable environments, but we propose that incorporating this kind of information, more specifically about the ITV of patterns of biomass allocation, provides valuable qualitative information, which would allow advancing the acclimation potential of species to particular field conditions. This information could improve the selection of species that would better fit each scenario of restoration, accounting for local and specific environmental pressures. For example, *Guazuma* is a highly flexible fast-growing species that could be ideal in most scenarios of TDF restoration, such as those in degraded pastures with variable nutrient availability. The pattern of *Vachellia* growth is more rigid but is better able to cope with herbivory, a key attribute in some of these situations in TDFs. In contrast, the greater height and more balanced pattern of *Enterolobium* growth may be more appropriate for degraded TDFs in intermediate successional stages that require species enrichment or replacement. Therefore, what ultimately determines the best or the most valuable species depends on the accurate knowledge of the specificities of each restoration scenario.

Easily implemented and standardized greenhouse experiments with a small set of soft traits thus are an inexpensive way to obtain high-quality data on potentially interesting tree species. Notice that the low demand of technology, materials, and infrastructure and the ease of measurement are all key properties for the global reproducibility of these species assessments. Other important ecological drivers of trait

plasticity such as competition should also be taken into account, despite that in restoration scenarios they may be of lesser importance than in natural field conditions. Additionally, coupled field experiments incorporating direct measures of seedling survival may be instrumental to validate the predictions drawn from these greenhouse assessments of ITV. The public availability of these data after curation and synthesis would promote better restoration practices, reducing the costs of forest recovery and ultimately enhancing the delivery of the services provided by these valuable and alarmingly threatened ecosystems.

ACKNOWLEDGMENTS

This research was supported by the European Research Council Synergy grant ERC-2013-SyG 610028-IMBALANCE-P, the Spanish Government grant CGL2016-79835-P, the project D/026276/09 from the Spanish Agency for International Development Cooperation (AECID), and the Catalan Government grant SGR 2017-1005. G.P. was supported by a post-doctoral fellowship from the Ramon Areces Foundation. Jordi Martínez-Vilalta provided many useful comments from an earlier version of the manuscript. O.R.L. and G. P. contributed equally to this work. O.R.L., J.M.E., and G.P. designed the experiment. O.R.L. implemented the experiment and collected data. O.R.L. and G.P. conducted the data analyses, interpreted the results, and wrote the manuscript with substantial contributions from J.M.E. and J.P.

LITERATURE CITED

- Ågren, G. I., J. M. Wetterstedt, and M. F. Billberger. 2012. Nutrient limitation on terrestrial plant growth—modeling the interaction between nitrogen and phosphorus. *New Phytologist* 194:953–960.
- Banda, K., A. Delgado-Salinas, K. G. Dexter, R. Linares-Palomino, A. Oliveira-Filho, D. Prado, M. Pullan, C. Quintana, R. Riina, and G. M. Rodríguez. 2016. Plant diversity patterns in neotropical dry forests and their conservation implications. *Science* 353:1383–1387.
- Barrance, A., et al. 2003. Árboles de Centroamérica: un manual para extensionistas. Bib. Orton IICA/CATIE, Turrialba, Costa Rica.
- Bartoń, K. 2019. MuMIn: multi-Model Inference. R package version 1.43.6. <https://CRAN.R-project.org/package=MumIn>
- Bastin, J.-F., Y. Finegold, C. Garcia, D. Mollicone, M. Rezende, D. Routh, C. M. Zohner, and T. W.

- Crowther. 2019. The global tree restoration potential. *Science* 365:76–79.
- Blonder, B., C. Lamanna, C. Violle, and B. J. Enquist. 2014. The n-dimensional hypervolume. *Global Ecology and Biogeography* 23:595–609.
- Bradshaw, A. D. 2006. Unravelling phenotypic plasticity—why should we bother? *New Phytologist* 170:644–648.
- Brouwer, R. 1963. Some aspects of the equilibrium between overground and underground plant parts. *Jaarboek van het Instituut voor Biologisch en Scheikundig onderzoek aan Landbouwgewassen* 213:31–39.
- Butterfield, R. P. 1995. Promoting biodiversity: advances in evaluating native species for reforestation. *Forest Ecology and Management* 75:111–121.
- Campo, J., and C. Vázquez-Yanes. 2004. Effects of nutrient limitation on aboveground carbon dynamics during tropical dry forest regeneration in Yucatán, Mexico. *Ecosystems* 7:311–319.
- Ceccon, E., and P. Hernández. 2009. Seed rain dynamics following disturbance exclusion in a secondary tropical dry forest in Morelos, Mexico. *Revista de Biología Tropical* 57:257–269.
- Ceccon, E., S. Sánchez, and J. Campo. 2004. Tree seedling dynamics in two abandoned tropical dry forests of differing successional status in Yucatán, Mexico: a field experiment with N and P fertilization. *Plant Ecology* 170:277–285.
- Chapin, F. S., A. J. Bloom, C. B. Field, and R. H. Waring. 1987. Plant responses to multiple environmental factors. *BioScience* 37:49–57.
- Chazdon, R. L., et al. 2016. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Science Advances* 2: e1501639.
- Díaz, S., J. Kattge, J. H. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth, and I. C. Prentice. 2016. The global spectrum of plant form and function. *Nature* 529:167–171.
- Esquivel, M. J., C. A. Harvey, B. Finegan, F. Casanoves, and C. Skarpe. 2008. Effects of pasture management on the natural regeneration of neotropical trees. *Journal of Applied Ecology* 45:371–380.
- Fatichi, S., S. Leuzinger, and C. Körner. 2014. Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling. *New Phytologist* 201:1086–1095.
- Gedroc, J. J., K. D. M. McConnaughay, and J. S. Coleman. 1996. Plasticity in root/shoot partitioning: Optimal, ontogenetic, or both? *Functional Ecology* 10:44–50.
- Gei, M., et al. 2018. Legume abundance along successional and rainfall gradients in Neotropical forests. *Nature Ecology & Evolution* 2:1104–1111.
- Gillespie, T. W., A. Grijalva, and C. N. Farris. 2000. Diversity, composition, and structure of tropical dry forests in Central America. *Plant Ecology* 147:37–47.
- Holl, K. 2012. Restoration of Tropical Forests. Pages 103–114. *in* Restoration ecology: the new frontier. John Wiley & Sons, Garsington Road, Oxford, UK.
- Holl, K. D., and E. Quiros-Nietzen. 1999. The effect of rabbit herbivory on reforestation of abandoned pasture in southern Costa Rica. *Biological Conservation* 87:391–395.
- IPCC [Intergovernmental Panel on Climate Change]. 2018. Summary for policymakers. Page 32 *in* V. Masson-Delmotte, et al. editors, Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. United Nations (UN), Geneva, Switzerland.
- Johnson, I. R., and J. H. M. Thornley. 1987. A Model of Shoot: root Partitioning with Optimal Growth. *Annals of Botany* 60:133–142.
- Kauffman, J. B., R. L. Sanford Jr, D. L. Cummings, I. Salcedo, and E. Sampaio. 1993. Biomass and nutrient dynamics associated with slash fires in neotropical dry forests. *Ecology* 74:140–151.
- Kitajima, K., and M. Fenner. 2000. Ecology of seedling regeneration. Pages 331–359 *in* Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford, UK.
- Lebrija-Trejos, E., J. A. Meave, L. Poorter, E. A. Pérez-García, and F. Bongers. 2010. Pathways, mechanisms and predictability of vegetation change during tropical dry forest succession. *Perspectives in Plant Ecology, Evolution and Systematics* 12:267–275.
- Ledo, A., K. I. Paul, D. F. Burslem, J. J. Ewel, C. Barton, M. Battaglia, K. Brooksbank, J. Carter, T. H. Eid, and J. R. England. 2018. Tree size and climatic water deficit control root to shoot ratio in individual trees globally. *New Phytologist* 217:8–11.
- Lenth, R. 2019. emmeans: estimated marginal means, aka least-squares means. R package version 1.3.5.1. <https://CRAN.R-project.org/package=emmeans>
- Lewis, S. L., C. E. Wheeler, E. T. Mitchard, and A. Koch. 2019. Restoring natural forests is the best way to remove atmospheric carbon. *Nature* 568:25–28.
- Lieberman, D. 1982. Seasonality and phenology in a dry tropical forest in Ghana. *Journal of Ecology* 70:791–806.
- Lieberman, D., and M. Li. 1992. Seedling recruitment patterns in a tropical dry forest in Ghana. *Journal of Vegetation Science* 3:375–382.

- Lloret, F., C. Casanovas, and J. Peñuelas. 1999. Seedling survival of Mediterranean shrubland species in relation to root: shoot ratio, seed size and water and nitrogen use. *Functional Ecology* 13:210–216.
- Markestijn, L., and L. Poorter. 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought-and shade-tolerance. *Journal of Ecology* 97:311–325.
- McMurtrie, R. E., R. J. Norby, B. E. Medlyn, R. C. Dewar, D. A. Pepper, P. B. Reich, and C. V. Barton. 2008. Why is plant-growth response to elevated CO₂ amplified when water is limiting, but reduced when nitrogen is limiting? A growth-optimisation hypothesis. *Functional Plant Biology* 35:521–534.
- Miles, L., A. C. Newton, R. S. DeFries, C. Ravilious, I. May, S. Blyth, V. Kapos, and J. E. Gordon. 2006. A global overview of the conservation status of tropical dry forests. *Journal of Biogeography* 33:491–505.
- Murphy, P., and A. Lugo. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17:67–88.
- Paine, C. T., L. Amisshah, H. Auge, C. Baraloto, M. Baruffol, N. Bourland, H. Bruelheide, K. Dainou, R. C. de Gouvenain, and J. L. Doucet. 2015. Globally, functional traits are weak predictors of juvenile tree growth, and we do not know why. *Journal of Ecology* 103:978–989.
- Peguero, G., and J. M. Espelta. 2011. Disturbance intensity and seasonality affect the resprouting ability of the neotropical dry-forest tree *Acacia pennatula*: Do resources stored below-ground matter? *Journal of Tropical Ecology* 27:539–546.
- Peguero, G., and J. M. Espelta. 2013. Evidence for insect seed predator dynamics mediated by vertebrate frugivores. *Revista Chilena de Historia Natural* 86:161–167.
- Peguero, G., O. R. Lanuza, R. Savé and J. M. Espelta. 2012. Allelopathic potential of the neotropical dry-forest tree *Acacia pennatula* Benth.: Inhibition of seedling establishment exceeds facilitation under tree canopies. *Plant Ecology* 213:1945–1953.
- Pérez-Harguindeguy, N., et al. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* 61:167–234.
- Poorter, L., C. V. Castilho, J. Schiatti, R. S. Oliveira, and F. R. Costa. 2018. Can traits predict individual growth performance? A test in a hyperdiverse tropical forest. *New Phytologist* 219:109–121.
- Poorter, H., and O. Nagel. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO₂, nutrients and water: a quantitative review. *Functional Plant Biology* 27:1191–1191.
- Poorter, H., K. J. Niklas, P. B. Reich, J. Oleksyn, P. Poot, and L. Mommer. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* 193:30–50.
- Poorter, L., D. M. Rozendaal, F. Bongers, J. S. de Almeida-Cortez, A. M. A. Zambrano, F. S. Álvarez, J. L. Andrade, L. F. A. Villa, P. Balvanera, and J. M. Becknell. 2019. Wet and dry tropical forests show opposite successional pathways in wood density but converge over time. *Nature Ecology & Evolution* 3:k928–k934.
- R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reich, P. B. 2002. Root-shoot relations: Optimality in acclimation and adaptation or the “Emperor's new clothes”? Pages 314–338. *in* Plant roots: the hidden half. Marcel Dekker, New York, New York, USA.
- Santiago, L. S. 2015. Nutrient limitation of eco-physiological processes in tropical trees. *Trees* 29:1291–1300.
- Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9:671–675.
- Stevens, W. D., C. Ulloa, A. Pool, and O. M. Montiel. 2001. *Flora de Nicaragua*. Missouri Botanical Garden Press, St Louis, Missouri, USA.
- Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, New Jersey, USA.
- Valladares, F., and E. Gianoli. 2007. How much ecology do we need to know to restore Mediterranean ecosystems? *Restoration Ecology* 15:363–368.
- Valladares, F., E. Gianoli, and J. M. Gómez. 2007. Ecological limits to plant phenotypic plasticity. *New Phytologist* 176:749–763.
- Via, S. 1993. Adaptive phenotypic plasticity: Target or by-product of selection in a variable environment? *American Naturalist* 142:352–365.
- Vieira, D. L., and A. Scariot. 2006. Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecology* 14:11–20.
- Vilà-Cabrera, A., J. Martínez-Vilalta, and J. Retana. 2015. Functional trait variation along environmental gradients in temperate and Mediterranean trees. *Global Ecology and Biogeography* 24:1377–1389.
- Werden, L. K., P. Alvarado, S. Zarges, E. Calderon, E. M. Schilling, M. L. Gutiérrez, and J. S. Powers. 2018. Using soil amendments and plant functional traits to select native tropical dry forest species for the restoration of degraded Vertisols. *Journal of Applied Ecology* 55:1019–1028.
- Wright, S. J., J. B. Yavitt, N. Wurzburger, B. L. Turner, E. V. Tanner, E. J. Sayer, L. S. Santiago, M. Kaspari,

L. O. Hedin, and K. E. Harms. 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology* 92:1616–1625.

Yang, J., M. Cao, and N. G. Swenson. 2018. Why functional traits do not predict tree demographic rates. *Trends in Ecology & Evolution* 33:326–336.

DATA ACCESSIBILITY

All data supporting the results presented in this contribution are archived at figshare with the <https://doi.org/10.6084/m9.figshare.11600592> under CC0 license.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3052/full>