

Research



Cite this article: Werden LK, Averill C, Crowther TW, Calderón-Morales E, Toro L, Alvarado J. P, Gutiérrez L. M, Mallory DE, Powers JS. 2022 Below-ground traits mediate tree survival in a tropical dry forest restoration. *Phil. Trans. R. Soc. B* **378**: 20210067. <https://doi.org/10.1098/rstb.2021.0067>

Received: 4 March 2021

Accepted: 3 March 2022

One contribution of 20 to a theme issue 'Understanding forest landscape restoration: reinforcing scientific foundations for the UN Decade on Ecosystem Restoration'.

Subject Areas:

ecology, ecosystems, plant science

Keywords:

biomass allocation, growth rates, plant functional traits, root traits, trait coordination, Vertisol

Author for correspondence:

Leland K. Werden

e-mail: lwerden@gmail.com

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.6248839>.

Below-ground traits mediate tree survival in a tropical dry forest restoration

Leland K. Werden^{1,3,4}, Colin Averill⁴, Thomas W. Crowther⁴, Erick Calderón-Morales², Laura Toro¹, Pedro Alvarado J.⁵, Milena Gutiérrez L.⁵, Danielle E. Mallory⁶ and Jennifer S. Powers^{1,2}

¹Department of Plant and Microbial Biology, and ²Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN 55108, USA

³Lyon Arboretum and School of Life Sciences, University of Hawaii, Honolulu, HI 96822, USA

⁴Department of Environmental Systems Science, ETH Zürich, 8092 Zürich, Switzerland

⁵Estación Experimental Forestal Horizontes, Área de Conservación Guanacaste, Liberia, 8008 Costa Rica

⁶Independent Researcher, Zürich, Switzerland

ORCID LKW, 0000-0002-3579-4352; CA, 0000-0003-4035-7760; TWC, 0000-0001-5674-8913; EC-M, 0000-0002-6612-9136; JSP, 0000-0003-3451-4803

Reforestation is one of our most promising natural climate solutions, and one that addresses the looming biodiversity crisis. Tree planting can catalyse forest community reassembly in degraded landscapes where natural regeneration is slow, however, tree survival rates vary remarkably across projects. Building a trait-based framework for tree survival could streamline species selection in a way that generalizes across ecosystems, thereby increasing the effectiveness of the global restoration movement. We investigated how traits mediated seedling survival in a tropical dry forest restoration, and how traits were coordinated across plant structures. We examined growth and survival of 14 species for 2 years and measured six below-ground and 22 above-ground traits. Species-level survival ranged widely from 7.8% to 90.1%, and a model including growth rate, below-ground traits and their interaction explained more than 73% of this variation. A strong interaction between below-ground traits and growth rate indicated that selecting species with fast growth rates can promote establishment, but this effect was most apparent for species that invest in thick fine roots and deep root structures. Overall, results emphasize the prominent role of below-ground traits in determining early restoration outcomes, and highlight little above- and below-ground trait coordination, providing a path forward for tropical dry forest restoration efforts.

This article is part of the theme issue 'Understanding forest landscape restoration: reinforcing scientific foundations for the UN Decade on Ecosystem Restoration'.

1. Introduction

The reassembly of diverse forests is an important component in the fight against biodiversity loss and climate change [1]. Moreover, many countries and organizations have committed to develop large-scale forest landscape restoration projects as part of programmes such as the Bonn Challenge [2] and the Trillion Tree initiative (1t.org). It is therefore imperative that appropriate management interventions be applied and targeted to local conditions [3,4]. Natural regeneration is often an optimal strategy to promote the re-establishment of native species [5,6], yet in many degraded landscapes, planting trees is a necessary step in the re-establishment of local biodiversity [7]. Within such environments, survival rates can be particularly low in the early stages of tree development, and so species selection can be a key determinant of restoration outcomes [8,9]. Identifying mixtures of species that can establish and survive within harsh environmental conditions is critical to ensure effective long-term outcomes of active forest landscape restoration efforts. Moreover, increasing plant survival in restoration

projects across the globe is important to ensure that resources are efficiently allocated by countries committed to the UN Decade on Ecosystem Restoration (see <https://www.deca-deonrestoration.org/>).

Despite the importance of appropriate tree species selection for the success of restoration efforts, few studies have characterized the plant traits that are most effective at promoting survival within degraded landscapes. A long history of ecological literature highlights how the performance of plants is contingent upon the expression of traits that can confer a selective advantage under a given set of environmental conditions. A range of morphological, physiological and biochemical functional traits [10] can predict tropical plant growth under different environmental conditions [11,12]. Moreover, there have been calls to use functional traits to develop species mixes for tropical forest restoration [9,13]. Additionally, integrating local knowledge of species life-history traits (e.g. successional status) when designing restoration interventions can not only improve outcomes, but also ensure that culturally and economically important species are explicitly included in the design process [14]. Yet, applying this knowledge to predict the survival of seedlings within a restoration context remains a major challenge as trait expression, survival rates and their interactions can vary significantly at these initial stages of development. In particular, within tropical dry forests—the second largest forested tropical biome [15] and one of the most endangered ecosystems [16]—seedlings are exposed to strong dry seasons within the first year of growth, and survival in the initial years of development is imperative to ensure that restoration is effective in this system [17,18]. Globally, tropical dry forests have been extensively deforested [19]. It is estimated that 97% of remaining tropical dry forests are threatened by climate change and human activities [20], making them a top-priority for landscape scale restoration efforts. Recent work highlights how physiological leaf traits such as water-use efficiency can be key indicators of seedling survival during initial phases of development in both tropical dry [21] and wet forests [22]. As such, the selection of species mixtures with high community-weighted water-use efficiency could potentially improve early survival rates at the community level. Increasing survival at early restoration stages has direct consequences for the development of soil organic matter [23], canopy structure [24] and subsequent recruitment of other native species [25,26]. However, by focusing only on the linear correlations with a few plant traits, these studies cannot account for the majority of the variation in species survival rates, or identify the mixtures of trait combinations likely to promote the initial survival of seedlings in the long term.

Given the multitude of approaches that plants use to compete for space, light, water and nutrients within heterogeneous environments, it is rare that any single trait can directly predict tree survival rates in a given location [27]. However, certain traits can be indicative of general life-history strategies. In particular, the growth rate of trees is a well-described indicator of changes in community assembly over time, with fast-growing resource-demanding species dominating in early successional stages and being gradually replaced by slower-growing species with more efficient resource-use [28]. As such, differences between ‘acquisitive’ (i.e. typically fast-growing species that maximize resource capture and are sensitive to abiotic stress) and ‘conservative’ (i.e. typically slow-growing, stress-tolerant species with higher resource-use efficiency) functional strategies (*sensu* [27]) may provide a useful framework for

guiding species selection that leads to high establishment rates of planted seedlings within a restoration context. Indeed, in a tropical dry forest field experiment, Gerhardt [29] highlighted that within-species tree seedling survival increased with higher height increment growth rates. However, although this ‘acquisitive’ growth strategy may promote tree survival within early stages of succession, rapid growth can often come at the expense of more ‘conservative’ strategies (e.g. that can be critical for species survival in harsh dry conditions).

In tropical dry forests, tree growth and survival are strongly limited by seasonal water availability [30], and species survival may be tightly linked to the successful development of deep, robust rooting systems [31]. However, while below-ground plant traits have been linked with plant vital rates (e.g. survival and growth) across terrestrial ecosystems, these traits are rarely considered when evaluating plant performance, especially in the context of restoration [32]. If investment in fast above-ground growth (i.e. acquisitive strategy) comes at the expense of plant investment in thicker absorptive fine roots and deeper supporting root systems (i.e. conservative strategy), then it may potentially limit seedling survival within tropical dry forest. Yet, until now, no study has explored the relative importance of below-ground traits relative to above-ground traits, or the trade-offs between trait combinations, that may be essential for improving species selection to promote increased survival rates within tropical dry forest restoration.

In this study, we examined growth and survival of 14 native tree species (840 seedlings in total) within a tropical dry forest restoration experiment in Costa Rica. These species are common in early successional forests in the region, are inclusive of the most dominant tree families [33] and encompass a wide range of life-history and resource-use traits [34]. Across all species, we measured six below-ground and 22 above-ground traits used to place species on leaf, stem and root economic trait spectra so that we could group trait values onto an acquisitive to conservative gradient [35], then examined how interspecific trait variation corresponds to species survival rates over the first 2 years of seedling growth. By examining the interactions between trait complexes, we test the relative importance of above- versus below-ground traits, and examine how interactions between trait combinations mediate seedling survival rates. Last, we investigated if trait syndromes (i.e. fast versus slow [35]) are coordinated across above- and below-ground organs, an area of open debate for tree species [36]. Ultimately, by taking a broad scope, we aim to identify a clear hierarchy of traits that should be considered in order to promote the survival of planted seedlings within tropical dry forest restoration.

2. Material and methods

(a) Study system

Our study was conducted at Estación Experimental Forestal Horizontes (10.712N, 85.594W) in Área de Conservación Guanacaste (ACG) in northwest Costa Rica. This tropical dry forest has a mean annual precipitation of 1730 mm, mean annual temperature of 25°C and a strong five- to six-month dry season from November to May, with little to no rainfall (http://www.investigadoresacg.org/main_eng.html). The study site was previously used for cattle grazing and agricultural crop production for decades, similar to land use in other tropical dry forests across Central America

Table 1. The 14 focal tropical dry forest tree species from the restoration experiment, their life-history traits, final survival percentages and relative height growth rates (RGR) over 2 years. Trait abbreviations are as follows: dispersal syndrome (W, wind; A, animal), leaf habit (D, deciduous; EG, evergreen), leaf compoundness (S, simple; C, compound).

species	family	dispersal syndrome	leaf habit	leaf compoundness	nitrogen fixer	survival (%)	RGR (ln(cm) d ⁻¹) *1000)
<i>Albizia saman</i>	Fabaceae	A	D	C	yes	13.4	1.15
<i>Cochlospermum vitifolium</i>	Bixaceae	W	D	S	no	7.8	0.77
<i>Cordia alliodora</i>	Boraginaceae	W	D	S	no	19.4	1.17
<i>Crescentia alata</i>	Bignoniaceae	A	D	S	no	90.1	1.86
<i>Dalbergia retusa</i>	Fabaceae	W	D	C	yes	41.7	1.87
<i>Gliricidia sepium</i>	Fabaceae	W	D	C	yes	9.4	0.83
<i>Guazuma ulmifolia</i>	Malvaceae	A	D	S	no	33.6	1.22
<i>Hymenaea courbaril</i>	Fabaceae	A	D	C	no	13.1	0.50
<i>Luehea candida</i>	Malvaceae	W	D	S	no	15.3	0.99
<i>Lysiloma divaricatum</i>	Fabaceae	W	D	C	yes	48.3	1.32
<i>Rehdera trinervis</i>	Verbenaceae	W	D	S	no	57.7	1.38
<i>Simarouba glauca</i>	Simaroubaceae	A	EG	C	no	38.8	1.14
<i>Tabebuia rosea</i>	Bignoniaceae	W	D	C	no	73.6	1.32
<i>Thouinidium decandrum</i>	Sapindaceae	W	D	C	no	19.1	1.75

[37] and the globe [19]. Succession is arrested in the study area, which had been regenerating for approximately 28 years before management intervention, due to intensive use that both compacted the soil and led to nutrient depletion [38]. As a result, the study site is dominated by only three tree species, *Cochlospermum vitifolium* (Bixaceae), *Crescentia alata* (Bignoniaceae) and *Guazuma ulmifolia* (Malvaceae) [38], making it particularly species-poor given that more than 60 tree species are observed in nearby forest inventory plots [39].

(b) Experimental design and species-level survival and growth

Here we report new observations of above- and below-ground plant functional traits that complement published data on seedling survival and growth in an experimental species selection trial [38]. Our original experiment aimed to determine how above-ground traits and soil amendments can be used to improve restoration outcomes in degraded Vertisols. Vertisols are soils that impede regeneration due to high shrink-swell clay content that leads to cracks in the dry season and flooding in the wet season [40]. In brief, in September 2014 we planted approximately 60 individuals of 32 native tropical dry forest tree species ($N = 1710$ seedlings) common across this landscape [33] and that have a wide range of functional strategies [34]. Seedlings were grown in an on-site nursery, and we accounted for intraspecific variation by collecting seeds across the ACG from at least three trees per species separated by at least 1 km. Seedlings were planted at 1×1 m spacing, with each species planted randomly in rows across four soil amendment (hydrogel, rice hulls, rice hull ash, sand) and two control blocks. Previous results showed that soil amendments did not influence survival or growth of seedlings after 2 years, so we do not consider this factor in the current study. Seedling competition with remnant vegetation (e.g. exotic forage grasses) was minimized by fully clearing around all seedlings with machetes at regular intervals (October and November 2014, and July 2015). We conducted the current study with species ($N = 14$) that had least three surviving individuals 2 years after planting (table 1).

We leveraged data collected in the original experiment to calculate species-level survival and growth rate for 14 species [38]. We made an effort to control for the influence of plant size on calculated species-level growth rates by initiating production of all species in the nursery at the same time. Mean planted seedling heights were similar at the species-level both when initially planted (*mean*: 29.8 cm; *s.d.*: 13.7) and after 2 years when harvests were made (*mean*: 72.9 cm; *s.d.*: 25.6). As such, we effectively compared growth rates between species computed from similarly sized seedlings. We calculated final species-level survival percentages and average relative height growth rate (RGR; $\ln(\text{cm}) \text{d}^{-1}$) after 2 years (two full growing and dry seasons; September 2014–June 2016) on 60 seedlings per species ($N = 840$). RGR was calculated using the standard equation: $(\ln[\text{final height}] - \ln[\text{initial height}]) / (\text{final day} - \text{initial day})$ [41] and assumptions for this approach were met (i.e. RGR did not slow or approach an asymptote over time). In July and August of 2016, we measured physiological traits and whole-plant structural characteristics *in situ*, then harvested both above- and below-ground biomass of two-year-old seedlings of each species (electronic supplementary material, figure S1). All measurements were made on three individuals of each species ($N = 42$ individuals total; see electronic supplementary material, table S1 for above- and below-ground trait list).

(c) *In situ* physiological measurements

Physiological traits related to photosynthesis and water-use were made on individuals in the field prior to destructive harvests. We used an LCI portable photosynthesis system (ADC Bioscientific Ltd, Hoddesdon, UK) to measure maximum photosynthetic capacity at 1200 par (A_{max} ; $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$), transpiration (E ; $\text{mmol m}^{-2} \text{s}^{-1}$) and instantaneous water-use efficiency (WUE ; $\mu\text{mol CO}_2 \text{mmol H}_2\text{O}^{-1}$). Next, we measured the change in leaf water potential (Ψ) from pre-dawn to mid-day (Ψ_{diurnal} ; MPa) to place species on a drought-tolerator versus avoider spectrum [42]. We measured pre-dawn and mid-day Ψ on two leaves per seedling with a Scholander pressure chamber (1505D, PMS Instruments, Albany, OR, USA), then calculated Ψ_{diurnal} .

(d) Full seedling measurements and harvests

For all harvested seedlings ($N = 3$ per species), we quantified a suite of above- and below-ground functional traits related to resource acquisition and stress tolerance. This sample size did not allow for intraspecific comparisons; however, we were able to compare how an extensive suite of above- and below-ground traits differed concurrently between many focal species using principal component analysis. In the field, we measured the crown radius (cm) by measuring from the seedling stem to the tip of the furthest leaf, then excavated whole seedlings taking care to harvest the entire root system, including all fine roots (roots ≤ 2 mm diameter). During harvests we measured the maximum lateral rooting extent by measuring from the base of each seedling to the end of the furthest excavated fine root tip (root lateral extent; cm) and maximum depth of the deepest fine root (root depth; cm). No harvested seedlings were observed competing for either above- (i.e. no overlapping canopies) or below-ground resources (i.e. no overlapping root structures) with adjacent seedlings.

We washed then scanned all fresh fine roots (absorptive first- and second-order roots ≤ 2 mm diameter; functional classification *sensu* [43]) to calculate fine root traits for each individual with a transparency scanner (Epson Perfection V800, Suwa, Japan; 2–4 images per individual), placing roots in a clear polycarbonate tray filled with water to ensure no root overlap. We used IJ_Rhizo [44] to calculate mean fine root diameter from scanned images. We then dried roots and calculated specific root length (SRL; m g^{-1}) and tissue density (RTD, g cm^{-3}) using total fine root length and volume calculated from images.

On three fresh leaves per harvested individual ($N = 126$ leaves total) we measured petiole length (mm) and leaf thickness (mm), then scanned and calculated leaf area (cm^2) with IMAGEJ [45]. To quantify whole-plant light capture capacity we scanned all fresh leaves of each individual and calculated whole canopy leaf area (total leaf area; cm^2) and leaf perimeter (total leaf perimeter; cm). We then dried all leaves at 60°C to constant weight and calculated specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$) and leaf density (g cm^{-3}). We bulked these leaves per individual and transported them to the University of Minnesota, where they were ground and analysed for foliar carbon to nitrogen ratio (C:N) and stable isotopes ($\delta^{13}\text{C}$; ‰).

Last, for each harvested individual, we dried all plant parts (leaves, stems, roots) to constant weight at 60°C and determined their mass (g), then calculated leaf (LMF), stem (SMF) and root (RMF) mass fractions for each seedling. In final individual-level biomass calculations, we included the mass of all leaves and roots used to quantify all traits above. For all species, we compiled a list of life-history traits from a previous study in the region [34]: dispersal syndrome (wind or animal), leaf habit (deciduous or evergreen), leaf compoundness (simple or compound), nitrogen-fixing status (fixer or non-fixer), seed mass (g) and stem wood density (g cm^{-3}). We calculated species-level trait means for statistical analyses (electronic supplementary material, table S2).

(e) Statistical analysis

In an effort to consider all above- or below-ground traits simultaneously, we performed principal component analysis, using the *prcomp* function within R statistical software [46]. All variables were centred and scaled relative to their means and variances to facilitate interpretation of principal components. We performed two principal component analyses, one using all above-ground traits, and a second using all below-ground traits. This generated two sets of species-level principal components which reflected variation in above- and below-ground traits, respectively.

We analysed survival rates at the species level using Bayesian phylogenetic generalized linear models (GLM) to account for

species relatedness, via the MCMCglmm function in R [47] and a phylogeny built with V.PhyloMaker [48]. Tree species survival rates were logit-transformed prior to analysis, as raw proportional data violate the assumption of homoscedasticity [49]. To ensure that results were equivalent to using non-transformed survival values, we compared the logit-transformed Bayesian phylogenetic GLMs to beta GLMs and found that model fits and results were almost identical (electronic supplementary material, figure S2 and table S3). To understand how relative growth rate, above-ground traits, below-ground traits and potential interactions influenced species-level survival rates we fit five statistical models. We focused on predicting species' survival rates rather than growth rates as the goal of our study was to develop a framework for restoration species selection that optimizes initial survival of planted seedlings. The first three models were univariate regressions between survival rate and either relative growth rate, the first principal component (PC1) of above-ground trait variation, or PC1 of below-ground trait variation. Then, we considered potential interactions between relative growth rate and trait principal components by fitting models with relative growth rate, PC1 of above- or below-ground trait variation, and their interaction, respectively.

- (1) Survival rate \sim above-ground PC1
- (2) Survival rate \sim below-ground PC1
- (3) Survival rate \sim relative growth rate (RGR)
- (4) Survival rate \sim RGR + above-ground PC1 + RGR * above-ground PC1
- (5) Survival rate \sim RGR + below-ground PC1 + RGR * below-ground PC1

We explored how additional principal components of above- and below-ground trait variation influenced survival rates, but these models performed substantially worse than models fit with the first principal component, and so were excluded from further investigation. Additionally, we performed a 'whole-plant traits' PCA including all above- and below-ground traits, however, PC1 of this PCA only described slightly more variation in survival than above-ground traits PC1, and far less variation than the below-ground traits PC1, so it was excluded from analyses. To determine the extent to which traits were coordinated across plant organs, we calculated pairwise Pearson's correlation coefficients (r) with bootstrapped standard errors and p -values (10 000 samples) between all continuous above- and below-ground functional traits.

3. Results

Survival to 2 years varied from 7.8% to 90.1% among species. Overall, relative growth rate was the strongest single predictor of tree species survival rate ($R^2_{\text{adj}} = 0.42$), indicating that species with faster growth rates typically had higher survival. However, PC1, which captured the greatest amount of variation in either above- or below-ground traits on their own, were poor predictors of tree species survival. However, when relative growth rate and tree species traits were considered in combination (relative growth rate, PC1 of below-ground trait variation and their interaction), variance explained increased by approximately 32% compared to models fit with relative growth rate alone ($R^2_{\text{adj}} = 0.73$ versus $R^2_{\text{adj}} = 0.41$, respectively). By contrast, models fit with relative growth rate, PC1 of above-ground trait variation and their interaction slightly decreased model R^2_{adj} relative to a model fit with relative growth rate alone (adjusted $R^2_{\text{adj}} = 0.28$, figure 1).

To better understand how the PC1s of above- and below-ground trait variation are driven by individual traits, we visualized bi-plots of principal component analyses with

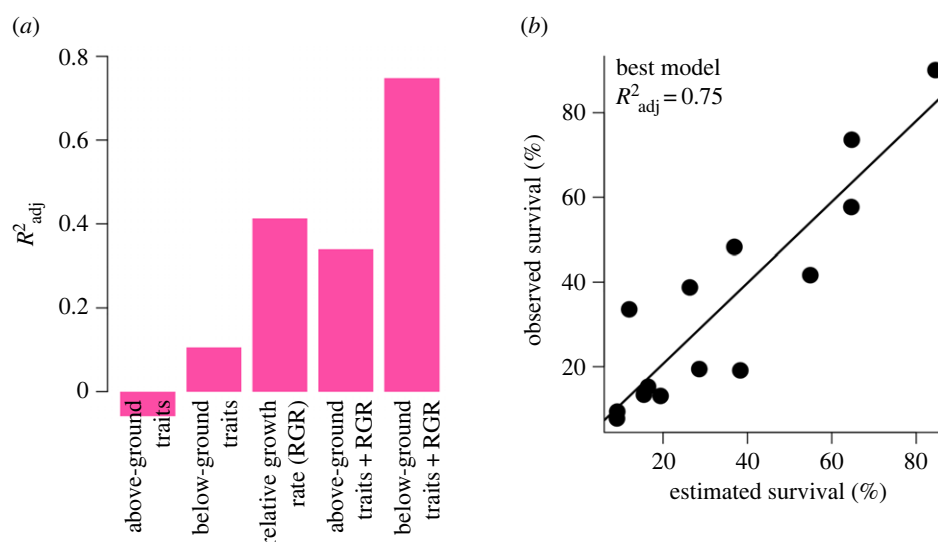


Figure 1. (a) R^2_{adj} of phylogenetically corrected tree species survival models as a function of the first principal component of above-ground trait variation, the first principal component of below-ground trait variation, relative growth rate (RGR), or interactions between RGR and respective above- or below-ground principal components. (b) Predicted versus observed species-level survival of the best model (fitted using RGR), the first principal component of below-ground trait variation and their interaction. (Online version in colour.)

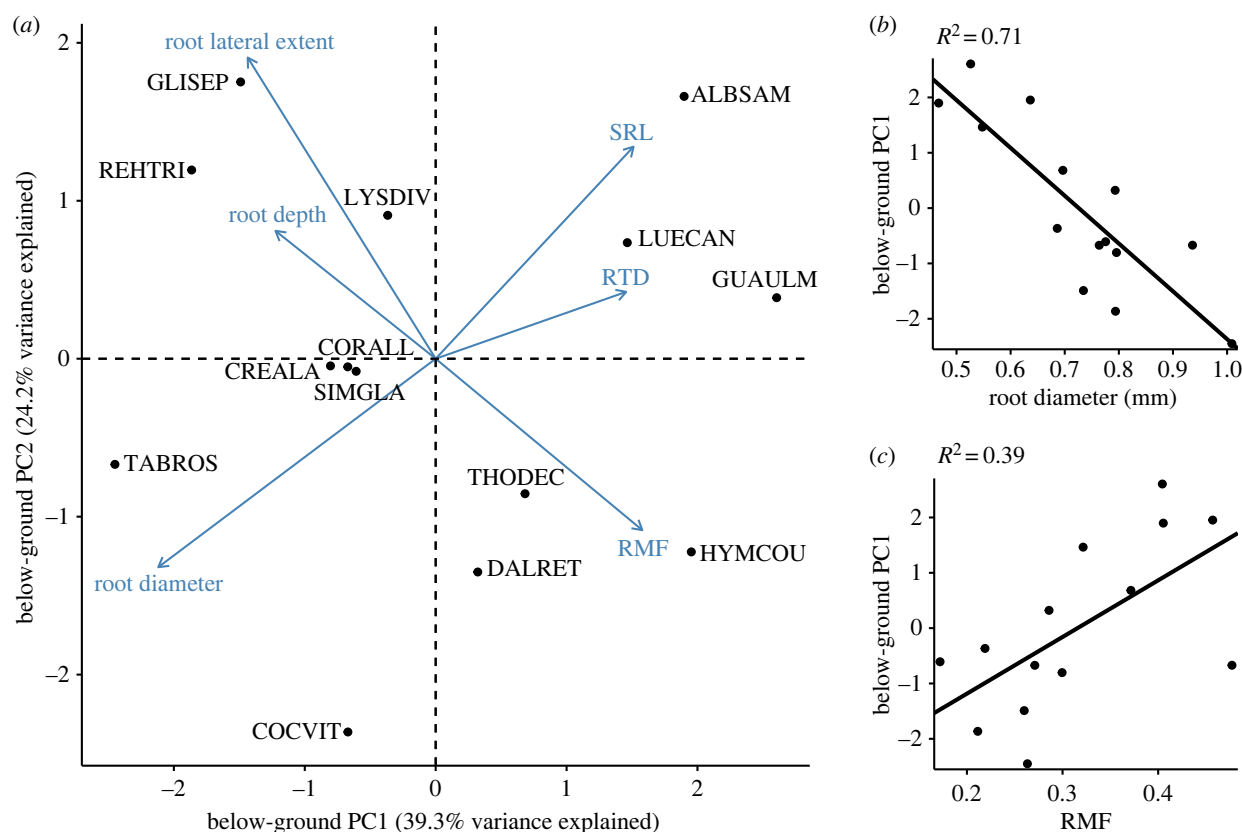


Figure 2. (a) Bi-plot of principal component analysis of tree species below-ground trait variation. (b,c) The two root traits which best correlate with the first principal component of below-ground trait variation, PC1. Root diameter is the average diameter of fine roots (mm). Root depth is the estimated maximum rooting depth of a species at 2 years (cm). RMF, root mass fraction; RTD, root tissue density; SRL specific root length. Species names are abbreviated with the first three letters of genus and first three letters of specific epithet. (Online version in colour.)

covariate vectors superimposed, as well univariate regressions between four traits that best correlated with PC1 within each analysis (figures 2 and 3; see electronic supplementary material, table S4 for variable contributions to and correlations with PC1). Below-ground trait variation was dominated by a trade-off between either having thick fine roots (high values of fine root diameter) or high biomass

allocation to roots (root mass fraction), greater root length per unit root mass (SRL) and higher root tissue density (figure 2). Above-ground trait variation was dominated by a trade-off between low versus high values of total leaf area and perimeter, crown radius and $\delta^{13}\text{C}$ (figure 3).

To evaluate the interaction between below-ground traits and relative growth rates, we used the fitted model to

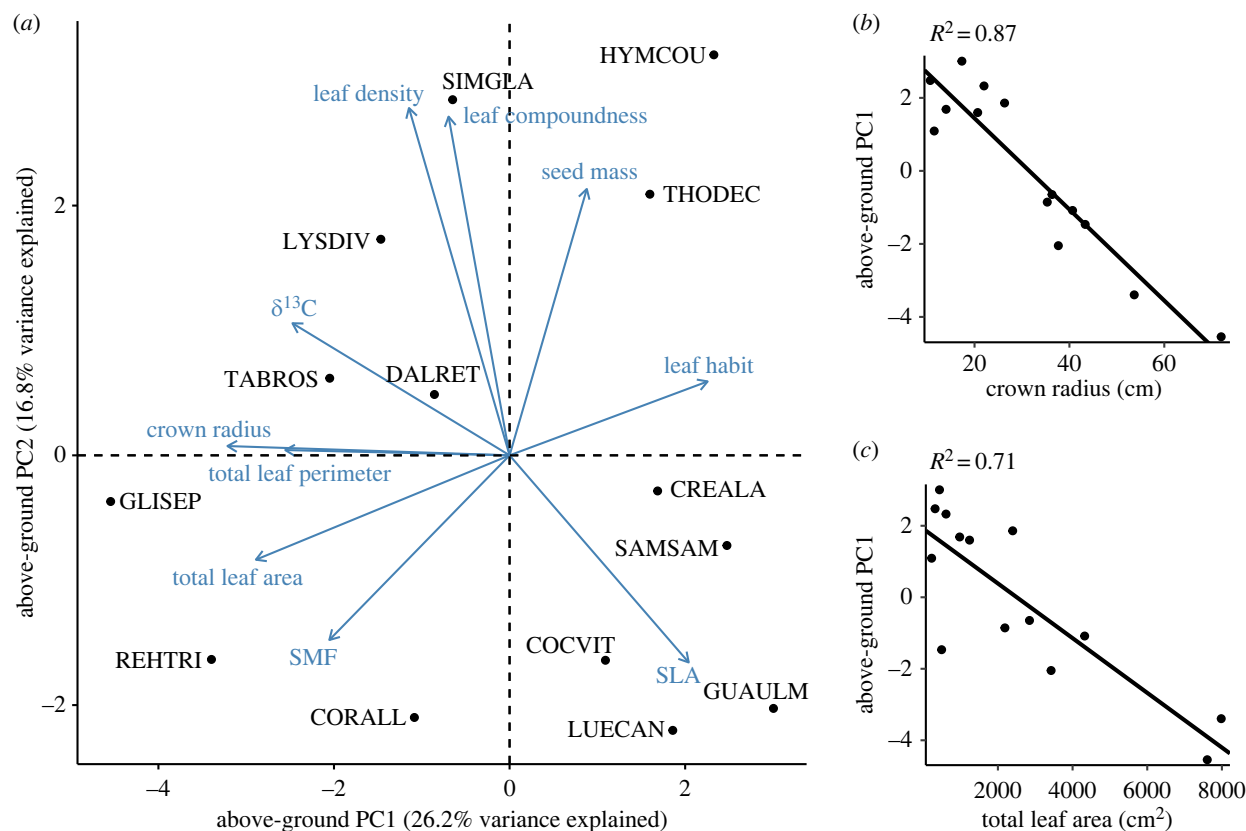


Figure 3. (a) Bi-plot of principal component analysis of tree species above-ground trait variation. Loadings for the 10 functional traits with the highest contributions are plotted. (b,c) The two above-ground traits that best correlate with the first principal component of above-ground trait variation, PC1. SLA, specific leaf area; SMF, stem mass fraction. Species names are abbreviated with the first three letters of genus and first three letters of specific epithet. (Online version in colour.)

develop an interaction plot that allowed us to vary relative growth rate at fixed levels of below-ground PC1. We varied relative growth rate from its 5% to 95% quantile in the dataset, and then set below-ground trait PC1 at either its 5%, 50% or 95% quantile. The 95% quantile of below-ground trait PC1 reflects thick fine roots and deeper maximum rooting depth, but lower root allocation and root tissue density. We refer to the 95%, 50% and 5% quantiles of PC1 as 'conservative', 'average' and 'acquisitive' below-ground trait syndromes, respectively. We observed that the interaction between relative growth rate and below-ground trait variation has a strong effect on estimated tree species survival rates, so much so that trees with otherwise high relative growth rates have much lower survival rates if those trees also have thin fine roots and high overall biomass allocation to roots (figure 4).

To examine trait coordination between plant organs, we generated a correlation matrix of pairwise Pearson's correlations between above- and below-ground traits (electronic supplementary material, figure S3). Root traits were largely not correlated with above-ground traits; however, some patterns emerged with respect to biomass allocation. Notably, no above-ground traits were correlated with root diameter, and only one above-ground trait (SMF) was correlated with root depth (i.e. species with deeper roots allocated more resources to stems; $r = 0.60$). In the few cases where SRL and RTD correlated with above-ground traits, relationships were typically negative; however, species with high RTD generally had high stem wood density ($r = 0.69$). Species that allocated more biomass below-ground (i.e. higher RMF) had acquisitive leaves (i.e. higher SLA; $r = 0.66$), narrower crowns ($r = -0.74$) and allocated less resources to leaves

overall (i.e. lower LMF, lower total leaf area and perimeter; r of -0.58 , -0.61 and -0.65 , respectively). The opposite patterns were observed for species with high root lateral extent (i.e. lower SLA, larger crowns, higher total leaf perimeter and area; r of -0.54 , 0.78 , 0.75 and 0.76 , respectively) and these species also allocated more resources to stem biomass (i.e. higher SMF; $r = 0.73$).

4. Discussion

The selection of tree species remains a major challenge facing restoration projects in tropical dry forest. Given the harsh growing conditions, characterized by prolonged dry seasons, mortality rates can be exceptionally high in the first 2 years following seedling establishment [38,50]. Surviving this initial growth phase is key to ensure effective restoration outcomes. In this analysis, only 34% of planted seedlings survived this initial 2-year period. Yet, survival rates of different tree species ranged from 7.8 to 90.1%, highlighting that effective species selection is necessary to maximize the chances of initial seedling establishment when restoring this ecosystem type.

To explain this variation in survival rates among our species, we explored a range of above- and below-ground traits. The prominent role of relative growth rate in governing initial survival emerged strongly, explaining over 40% of the variation in survival rates alone (figure 1). Specifically, species able to tolerate conditions in this degraded soil and allocate resources to rapid initial height growth consistently established quickly and tended to survive throughout the initial 2-year growth phase. These findings are consistent

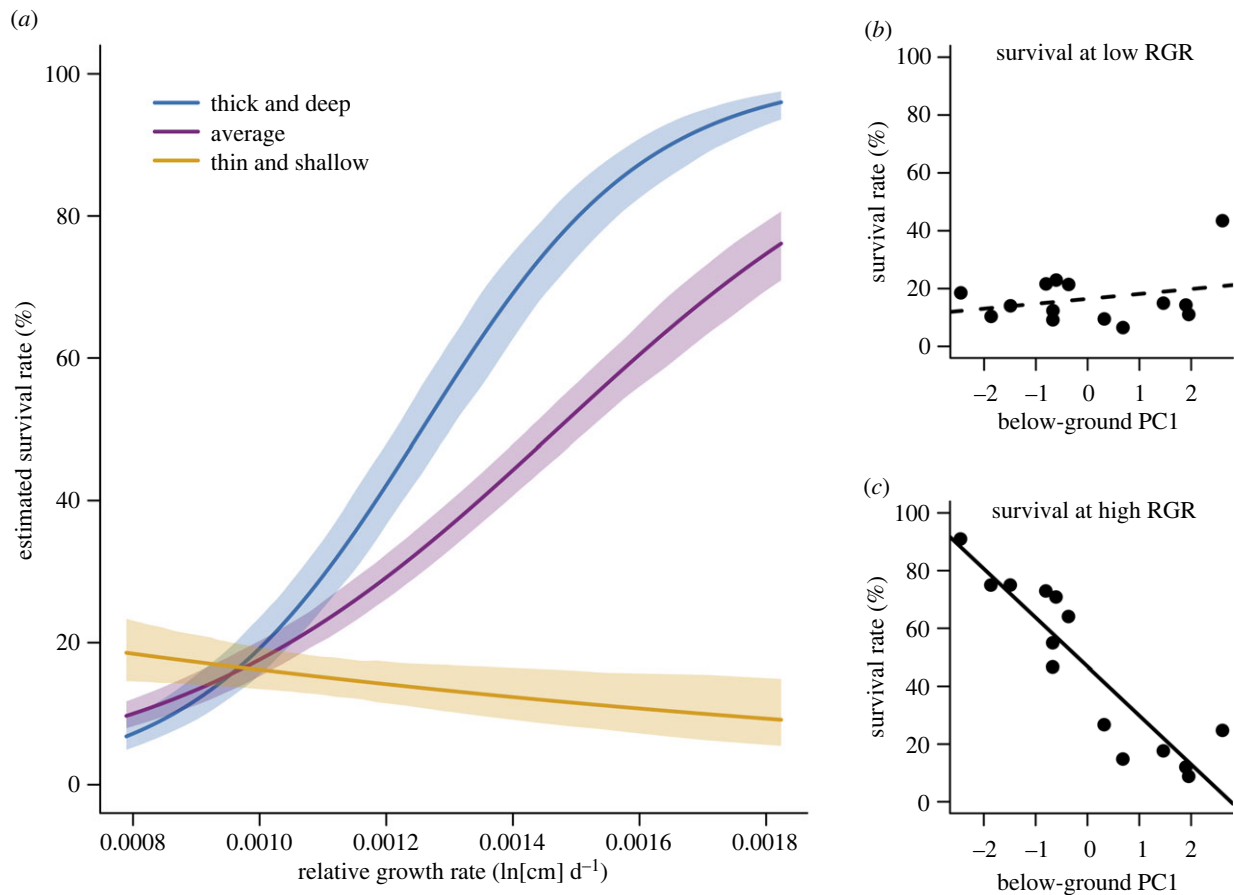


Figure 4. (a) Predicted tree species survival rates from the best-fitting phylogenetically corrected model across the range of relative growth rates observed within the dataset, while fixing below-ground trait PC1 values to their 5%, 50% or 95% quantiles within the dataset. The 95% quantile of PC1 (b) is correlated with comparatively thinner fine roots, shallower root structures and higher overall biomass allocation to roots compared with the 5% quantile (c), which we refer to as 'conservative' versus 'acquisitive' below-ground strategies, respectively. Shaded regions represent 1 s.e. of model estimates. (Online version in colour.)

with evidence from both tree planting efforts [51] and natural regeneration projects [29] in Neotropical tropical dry forests, highlighting that tropical dry forest seedling growth rates can be tightly and positively linked with survival for the first few years of establishment. Whereas the growth–mortality trade-off dictates that fast-growing species typically have the highest mortality rates in closed canopy forest [52], in these high light early successional environments this trade-off does not appear to hold (*also see* [53]). Therefore, in early stages of tropical dry forest restoration, acquisitive growth strategies clearly promote rapid establishment and seedling survival. This suggests that integrating fast-growing species that persist naturally at early successional stages into planting mixes is a straightforward approach towards improving restoration outcomes on extensively degraded sites where there is little to no extant canopy cover. Moreover, this pattern was not driven by nitrogen-fixing species included in our study, which can have much higher growth and survival than non-fixers in regenerating tropical wet forest [54] and can have higher growth than non-fixers in tropical wet forest restoration plantings [55]. Rather, both fixers and non-fixers were integrated along growth and survival gradients, highlighting that species with both strategies should be considered for species mixes. Indeed, ensuring that species mixes containing a wide range of functional groups with appropriate traits for a given situation can not only restore targeted ecosystem services, but also increase forest resilience to ongoing global environmental change [1].

Despite the important role of seedling growth rate in governing survival in this system, several species diverged strongly from this linear relationship, and the inclusion of functional traits considerably improved the capacity to predict overall survival rates across species. However, the importance of different traits varied considerably between above- and below-ground characteristics. Although the inclusion of above-ground traits did not significantly ($p > 0.05$) affect the model fit, the inclusion of below-ground traits considerably improved the predictive accuracy of our model. Specifically, the final model including relative growth rate, the PC1 for below-ground root traits and their interaction explained 73% of the variation in survival rates across our study species. While our results indicate that below-ground traits are highly predictive of initial survival rates in this system, survival rates over longer timescales may be dictated by different suites of traits, ontogeny [56] and/or cyclical climate cycles (e.g. El Niño and La Niña). This prominent role of below-ground traits in predicting initial species survival is consistent with the idea that root investment is critical for plant survival, especially in regions with limited water availability. Indeed, both broad- [57] and fine-scale [58] studies consistently highlight the importance of root investment within arid and seasonally dry regions, as the root : shoot ratio of plants tends to increase in drier conditions. Moreover, in this tropical dry forest, species that allocated more resources below-ground (i.e. higher RMF) allocated less resources to leaf construction (i.e. higher SLA), crown development and total canopy leaf

area (electronic supplementary material, figure S3). This trade-off is consistent with observations from Panama indicating that seedling growth in tropical dry forest was maximized when more resources were invested in roots versus leaves [59].

The specific nature of the relationships between root traits and species survival can provide mechanistic insights into their effects on seedling survival. Principal Component 1 for the below-ground traits correlates negatively with root depth, root diameter and root lateral extent and positively with RME, SRL and root tissue density (figure 2). As such, the negative overall relationship between PC1 and species survival indicates that investing in thicker fine roots, and developing deeper and more laterally extensive root structures can promote species survival within the initial years of seedling growth. These patterns appear to be tightly linked to the optimization of resource capture, and observations demonstrate that early successional tropical dry forest trees in Mexico typically have deep root structures that increase water foraging capacity [60]. Moreover, all of the species in this study associate with arbuscular mycorrhizal fungi and species with thicker fine roots typically have high mycorrhizal colonization rates [61], which could directly increase root surface area for nutrient and water uptake. Our findings likely hold across the dry tropics in forests dominated by deciduous species. However, in seasonal tropical forests with communities dominated by evergreen species, which inherently allocate more biomass to roots [62], other suites of traits may better differentiate between species when predicting initial seedling survival rates. Additionally, the low sample size of our seedling harvests may have limited our ability to well resolve trait means for specific species, potentially influencing observed trait syndrome \times growth rate interactions. However, our initial analysis highlights that integrating below-ground traits into restoration design is an important research direction, and further characterizing below-ground trait variation will only help to improve our understanding of this topic.

We also found a strong interaction between the effects of root investment and vertical growth rate in predicting overall survival rates. That is, fast-growing species had higher survival if they also had thick fine roots and deep root structures (figure 4). This interaction between root traits and growth rate is counterintuitive as these growth traits are often considered to be associated with distinctly opposing growth strategies. Specifically, fast vertical growth is generally considered to be associated with an 'acquisitive' growth strategy, whereas the investment in thick fine roots, and allocating resources to root structure development are often considered to occur in 'conservative' species. Therefore, to maximize initial survival rates in this tropical dry forest region, and in other tropical seasonal forests with strong dry seasons when little to no rain falls for four months or more, it is essential to select species that exhibit relatively acquisitive above-ground growth, with relatively conservative root structures. Thus, assigning binary resource-use strategies (acquisitive versus conservative) at the whole-plant level may be misleading when attempting to determine the drivers of plant performance in a restoration context. Moreover, below-ground traits were largely uncorrelated with or decoupled from above-ground traits in this system (electronic supplementary material, figure S3). This finding supports growing evidence that coordination across above- and below-ground organs in tree species may be limited [36,63]. However, there was some indication that wood and

root tissue densities were linked across species, a pattern that has also been observed across a broad range of Neotropical tree species [64]. Additionally, the traits tightly coupled with seedling survival in below-ground PC1 (root diameter and RME; figure 2) were only correlated with above-ground traits in one instance. Thus, our findings suggest that despite the difficulty associated with quantifying below-ground traits, investing time into these efforts and improving our capacity to predict species-level trait values out of sample (e.g. [65]) will most likely improve the design of tropical dry forest restorations. Moreover, large-scale forest biodiversity–ecosystem function experiments have demonstrated that maximizing functional diversity in planted forests promotes higher productivity [66] and increases resilience and ecosystem services [67]. Thus, ensuring that planted species mixes are highly diverse, in terms of both above- and below-ground functional attributes, is likely to be important, and using planting mixes with high species richness is a strategy demonstrated to meet this goal [68].

5. Conclusion

By highlighting the traits that predict tree seedling survival, our analysis provides a path forward for the selection of species to promote survival in tropical dry forest restoration efforts. Selecting species with fast vertical growth rates has the potential to promote rapid seedling establishment when planted into degraded Vertisols, but this effect is only apparent in species that also invest in thicker fine roots, and more extensive root structures. As such, this analysis highlights the importance of considering below-ground root characteristics, relative to above-ground stem and leaf traits, when predicting seedling survival within these seasonally dry ecosystems. Given the typically low seedling survival rates in tropical dry forests, these insights into species selection may potentially be invaluable for promoting the initial establishment of vegetation. By highlighting the key traits that promote seedling survival, our study can serve as a guideline to select species that can tolerate initial planting conditions in tropical dry forest restoration efforts.

Data accessibility. All survival and growth data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.fd57r> [69]. All functional trait data and code and data to reproduce analyses and figures are available from Figshare [70].

Supplementary material is available online [71].

Authors' contributions. L.K.W.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, validation, visualization, writing—original draft, writing—review and editing; C.A.: data curation, formal analysis, validation, visualization, writing—original draft, writing—review and editing; T.W.C.: data curation, formal analysis, writing—original draft, writing—review and editing; E.C.-M.: data curation, investigation, methodology, writing—review and editing; L.T.: data curation, investigation, writing—review and editing; P.A.J.: investigation, writing—review and editing; M.G.L.: conceptualization, project administration, writing—review and editing; D.M.: investigation, visualization; J.S.P.: conceptualization, funding acquisition, project administration, resources, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We have no competing interests.

Funding. L.K.W. was supported by GRFP (11-582) and DDIG (1600710) from the US National Science Foundation, and a Garden Club of America Tropical Botany Fellowship. C.A. was supported by Ambizione grant no. PZ00P3_17990 from the Swiss National Science Foundation.

Acknowledgements. We thank Daniel Perez A. for collecting seeds, S. Zarges for help collecting initial survival and growth data, Roger Blanco from Área de Conservación Guanacaste for facilitating this

work, and many volunteers for help planting the experiment. We thank three anonymous reviewers and L. Banin who provided excellent feedback that helped to improve our manuscript.

References

- Lamb D. 2018 Undertaking large-scale forest restoration to generate ecosystem services: landscape restoration and ecosystem services. *Restorat. Ecol.* **26**, 657–666. (doi:10.1111/rec.12706)
- Global Partnership on Forest Landscape Restoration. 2021 The Bonn Challenge. See <https://www.bonnchallenge.org/>.
- Holl KD, Aide TM. 2011 When and where to actively restore ecosystems? *For. Ecol. Manag.* **261**, 1558–1563. (doi:10.1016/j.foreco.2010.07.004)
- Jones HP *et al.* 2018 Restoration and repair of Earth's damaged ecosystems. *Proc. R. Soc. B* **285**, 20172577. (doi:10.1098/rspb.2017.2577)
- Chazdon RL. 2014 *Second growth: the promise of tropical forest regeneration in an age of deforestation*. Chicago, IL: University of Chicago Press.
- Crouzeilles R *et al.* 2020 Achieving cost-effective landscape-scale forest restoration through targeted natural regeneration. *Conserv. Lett.* **13**, 1–9. (doi:10.1111/conl.12709)
- Rodrigues RR, Lima RAF, Gandolfi S, Nave AG. 2009 On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. *Biol. Conserv.* **142**, 1242–1251. (doi:10.1016/j.biocon.2008.12.008)
- Lamb D. 2014 *Large-scale forest restoration*. Oxfordshire, UK: Routledge.
- Charles LS. 2018 Plant functional traits and species selection in tropical forest restoration. *Trop. Conserv. Sci.* **11**, 194008291878415. (doi:10.1177/1940082918784157)
- Vielle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007 Let the concept of trait be functional! *Oikos* **116**, 882–892. (doi:10.1111/j.0030-1299.2007.15559.x)
- Poorter L *et al.* 2008 Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology* **89**, 1908–1920. (doi:10.1890/07-0207.1)
- Visser MD, Bruijning M, Wright SJ, Muller-Landau HC, Jongejans E, Comita LS, de Kroon H. 2016 Functional traits as predictors of vital rates across the life cycle of tropical trees. *Funct. Ecol.* **30**, 168–180. (doi:10.1111/1365-2435.12621)
- Ostertag R, Warman L, Cordell S, Vitousek PM. 2015 Using plant functional traits to restore Hawaiian rainforest. *J. Appl. Ecol.* **52**, 805–809. (doi:10.1111/1365-2664.12413)
- Hastings Z, Ticktin T, Botelho M, Reppun N, Kukea-Shultz K, Wong M, Melone A, Bremer L. 2020 Integrating co-production and functional trait approaches for inclusive and scalable restoration solutions. *Conserv. Sci. Pract.* **2**, e250. (doi:10.1111/csp2.250)
- Murphy PG, Lugo AE. 1986 Ecology of tropical dry forest. *Annu. Rev. Ecol. Syst.* **17**, 67–88.
- Janzen DH. 2002 Tropical dry forest: Area de Conservación Guanacaste, northwestern Costa Rica. In *Handbook of ecological restoration* (eds MR Perrow, AJ Davey), pp. 559–583. Cambridge, UK: Cambridge University Press.
- Parrotta JA, Turnbull JW, Jones N. 1997 Catalyzing native forest regeneration on degraded tropical lands. *For. Ecol. Manag.* **99**, 1–7. (doi:10.1016/S0378-1127(97)00190-4)
- Campoe OC, Iannelli C, Stape JL, Cook RL, Mendes JCT, Vivian R. 2014 Atlantic forest tree species responses to silvicultural practices in a degraded pasture restoration plantation: from leaf physiology to survival and initial growth. *For. Ecol. Manag.* **313**, 233–242. (doi:10.1016/j.foreco.2013.11.016)
- Blackie R *et al.* 2014 Tropical dry forests: the state of global knowledge and recommendations for future research. Discussion Paper. *CIFOR, Bogor*.
- Miles L, Newton AC, DeFries RS, Ravilious C, May I, Blyth S, Kapos V, Gordon JE. 2006 A global overview of the conservation status of tropical dry forests. *J. Biogeogr.* **33**, 491–505. (doi:10.1111/j.1365-2699.2005.01424.x)
- Werden LK, Calderón-Morales E, Alvarado JP, Gutiérrez LM, Nedveck DA, Powers JS. 2020 Using large-scale tropical dry forest restoration to test successional theory. *Ecol. Appl.* **30**, e02116. (doi:10.1002/eap.2116)
- Guimarães ZTM, dos Santos VAHF, Nogueira WLP, Martins NO de A, Ferreira MJ. 2018 Leaf traits explaining the growth of tree species planted in a Central Amazonian disturbed area. *For. Ecol. Manag.* **430**, 618–628. (doi:10.1016/j.foreco.2018.08.048)
- Rodrigues Nogueira Jr L, De Moraes Gonçalves JL, Lex Engel V, Parrotta J. 2011 Soil dynamics and carbon stocks 10 years after restoration of degraded land using Atlantic Forest tree species. *For. Syst.* **20**, 536–545. (doi:10.5424/fs/20112003-11844)
- Zahawi RA, Dandois JP, Holl KD, Nadwodny D, Reid JL, Ellis EC. 2015 Using lightweight unmanned aerial vehicles to monitor tropical forest recovery. *Biol. Conserv.* **186**, 287–295. (doi:10.1016/j.biocon.2015.03.031)
- Holl KD, Reid JL, Chaves-Fallas JM, Oviedo-Brenes F, Zahawi RA. 2017 Local tropical forest restoration strategies affect tree recruitment more strongly than does landscape forest cover. *J. Appl. Ecol.* **54**, 1091–1099. (doi:10.1111/1365-2664.12814)
- de la Peña-Domene M, Martínez-Garza C, Howe HF. 2013 Early recruitment dynamics in tropical restoration. *Ecol. Appl.* **23**, 1124–1134. (doi:10.1890/12-1728.1)
- Laughlin DC. 2014 Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecol. Lett.* **17**, 771–784. (doi:10.1111/ele.12288)
- Bazzaz FA, Pickett STA. 1980 Physiological ecology of tropical succession: a comparative review. *Annu. Rev. Ecol. Syst.* **11**, 287–310. (doi:10.1146/annurev.es.11.110180.001443)
- Gerhardt K. 1996 Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. *For. Ecol. Manag.* **82**, 33–48. (doi:10.1016/0378-1127(95)03700-4)
- Engelbrecht BMJ, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL, Hubbell SP. 2007 Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* **447**, 80–82. (doi:10.1038/nature05747)
- Boonman CCF, Langevelde F van, Oliveras I, Couédon J, Luijken N, Martini D, Veenendaal EM. 2020 On the importance of root traits in seedlings of tropical tree species. *New Phytol.* **227**, 156–167. (doi:10.1111/nph.16370)
- Garbowski M *et al.* 2020 Getting to the root of restoration: considering root traits for improved restoration outcomes under drought and competition. *Restorat. Ecol.* **28**, 1384–1395. (doi:10.1111/rec.13291)
- Powers JS, Becknell JM, Irving J, Pérez-Aviles D. 2009 Diversity and structure of regenerating tropical dry forests in Costa Rica: geographic patterns and environmental drivers. *For. Ecol. Manag.* **258**, 959–970. (doi:10.1016/j.foreco.2008.10.036)
- Powers JS, Tiffin P. 2010 Plant functional type classifications in tropical dry forests in Costa Rica: leaf habit versus taxonomic approaches: leaf habit and functional traits of dry forest trees. *Funct. Ecol.* **24**, 927–936. (doi:10.1111/j.1365-2435.2010.01701.x)
- Reich PB. 2014 The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *J. Ecol.* **102**, 275–301. (doi:10.1111/1365-2745.12211)
- Weemstra M, Mommer L, Visser EJW, Ruijven J, Kuyper TW, Mohren GMJ, Sterck FJ. 2016 Towards a multidimensional root trait framework: a tree root review. *New Phytol.* **211**, 1159–1169. (doi:10.1111/nph.14003)
- Griscom HP, Ashton MS. 2011 Restoration of dry tropical forests in Central America: a review of pattern and process. *For. Ecol. Manag.* **261**, 1564–1579. (doi:10.1016/j.foreco.2010.08.027)

38. Werden LK, Alvarado J P, Zarges S, Calderón M E, Schilling EM, Gutiérrez L M, Powers JS. 2018 Using soil amendments and plant functional traits to select native tropical dry forest species for the restoration of degraded Vertisols. *J. Appl. Ecol.* **55**, 1019–1028. (doi:10.1111/1365-2664.12998)
39. Waring BG, Pérez-Aviles D, Murray JG, Powers JS. 2019 Plant community responses to stand-level nutrient fertilization in a secondary tropical dry forest. *Ecology* **100**, e02691. (doi:10.1002/ecy.2691)
40. Deckers J, Spaargaren O, Nachtergaele F. 2001 Vertisols: genesis, properties and soilscape management for sustainable development. In *The sustainable management of vertisols* (eds JK Syers, FWT Penning de Vries, P Nyamudeza), pp. 3–20. Wallingford, UK: CABI.
41. Hoffmann WA, Poorter H. 2002 Avoiding bias in calculations of relative growth rate. *Ann. Bot.* **90**, 37–42. (doi:10.1093/aob/mcf140)
42. Martínez-Vilalta J, Poyatos R, Aguadé D, Retana J, Mencuccini M. 2014 A new look at water transport regulation in plants. *New Phytol.* **204**, 105–115. (doi:10.1111/nph.12912)
43. McCormack ML *et al.* 2015 Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytol.* **207**, 505–518. (doi:10.1111/nph.13363)
44. Pierret A, Gonkhamdee S, Jourdan C, Maeght J-L. 2013 IJ_Rhizo: an open-source software to measure scanned images of root samples. *Plant Soil* **373**, 531–539. (doi:10.1007/s11104-013-1795-9)
45. Schneider CA, Rasband WS, Eliceiri KW. 2012 NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **9**, 671–675. (doi:10.1038/nmeth.2089)
46. R Development Core Team. 2020 *R: a language and environment for statistical computing. Version 4.0.3*. See <https://www.r-project.org/>.
47. Hadfield JD. 2010 MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Softw.* **33**, 1–22. (doi:10.18637/jss.v033.i02)
48. Jin Y, Qian H. 2019 VPhyloMaker: an R package that can generate very large phylogenies for vascular plants. *Ecography* **42**, 1353–1359. (doi:10.1111/ecog.04434)
49. Cribari-Neto F, Zeileis A. 2010 Beta Regression in R. *J. Stat. Softw.* **34**, 1–24. (doi:10.18637/jss.v034.i02)
50. Gerhardt K. 1993 Tree seedling development in tropical dry abandoned pasture and secondary forest in Costa Rica. *J. Veg. Sci.* **4**, 95–102. (doi:10.2307/3235736)
51. Carrasco-Carballido V, Martínez-Garza C, Jiménez-Hernández H, Márquez-Torres F, Campo J. 2019 Effects of initial soil properties on three-year performance of six tree species in tropical dry forest restoration plantings. *Forests* **10**, 428. (doi:10.3390/f10050428)
52. Wright SJ *et al.* 2010 Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* **91**, 11.
53. González-Tokman DM, Barradas VL, Boege K, Domínguez CA, del-Val E, Saucedo E, Martínez-Garza C. 2018 Performance of 11 tree species under different management treatments in restoration plantings in a tropical dry forest: tree performance in a tropical dry forest. *Restorat. Ecol.* **26**, 642–649. (doi:10.1111/rec.12617)
54. Menge DNL, Chazdon RL. 2016 Higher survival drives the success of nitrogen-fixing trees through succession in Costa Rican rainforests. *New Phytol.* **209**, 965–977.
55. Martínez-Garza C, Campo J, Ricker M, Tobón W. 2016 Effect of initial soil properties on six-year growth of 15 tree species in tropical restoration plantings. *Ecol. Evol.* **6**, 8686–8694. (doi:10.1002/ece3.2508)
56. Derroire G, Powers JS, Hulshof CM, Cárdenas Varela LE, Healey JR. 2018 Contrasting patterns of leaf trait variation among and within species during tropical dry forest succession in Costa Rica. *Sci. Rep.* **8**, 1–11. (doi:10.1038/s41598-017-18525-1)
57. Ledo A *et al.* 2018 Tree size and climatic water deficit control root to shoot ratio in individual trees globally. *New Phytol.* **217**, 8–11. (doi:10.1111/nph.14863)
58. Lieberman D, Li M. 1992 Seedling recruitment patterns in a tropical dry forest in Ghana. *J. Veg. Sci.* **3**, 375–382. (doi:10.2307/3235763)
59. Brenes-Arguedas T, Roddy AB, Kursar TA. 2013 Plant traits in relation to the performance and distribution of woody species in wet and dry tropical forest types in Panama. *Funct. Ecol.* **27**, 392–402. (doi:10.1111/1365-2435.12036)
60. Paz H, Pineda-García F, Pinzón-Pérez LF. 2015 Root depth and morphology in response to soil drought: comparing ecological groups along the secondary succession in a tropical dry forest. *Oecologia* **179**, 551–561. (doi:10.1007/s00442-015-3359-6)
61. McCormack ML, Iversen CM. 2019 Physical and functional constraints on viable belowground acquisition strategies. *Front. Plant Sci.* **10**, 1215. (doi:10.3389/fpls.2019.01215)
62. Smith-Martin CM, Xu X, Medvigy D, Schnitzer SA, Powers JS. 2020 Allometric scaling laws linking biomass and rooting depth vary across ontogeny and functional groups in tropical dry forest lianas and trees. *New Phytol.* **226**, 714–726. (doi:10.1111/nph.16275)
63. Valverde-Barrantes O, Smemo K, Blackwood C. 2015 Fine root morphology is phylogenetically structured, but nitrogen is related to the plant economics spectrum in temperate trees. *Funct. Ecol.* **29**, 796–807.
64. Fortunel C, Fine PVA, Baraloto C. 2012 Leaf, stem and root tissue strategies across 758 Neotropical tree species. *Funct. Ecol.* **26**, 1153–1161. (doi:10.1111/j.1365-2435.2012.02020.x)
65. Swenson NG. 2014 Phylogenetic imputation of plant functional trait databases. *Ecography* **37**, 105–110. (doi:10.1111/j.1600-0587.2013.00528.x)
66. Bongers FJ *et al.* 2021 Functional diversity effects on productivity increase with age in a forest biodiversity experiment. *Nat. Ecol. Evol.* **5**, 1594–1603. (doi:10.1038/s41559-021-01564-3)
67. Messier C *et al.* 2021 For the sake of resilience and multifunctionality, let's diversify planted forests! *Conserv. Lett.* **15**, e12829. (doi:10.1111/conl.12829)
68. Huang Y *et al.* 2018 Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science* **362**, 80–83. (doi:10.1126/science.aat6405)
69. Werden LK, Alvarado PJ, Zarges S, Calderón EM, Schilling EM, Gutiérrez ML, Powers JS. 2018 Data from: Using soil amendments and plant functional traits to select native tropical dry forest species for the restoration of degraded Vertisols. Dryad Digital Repository. (doi:10.5061/dryad.fd57r)
70. Werden LK, Averill C, Crowther TW, Calderón-Morales E, Toro L, Alvarado JP, Gutiérrez LM, Mallory DE, Powers JS. 2022 Data and code for: Below-ground traits mediate tree survival in a tropical dry forest restoration. Figshare. (doi:10.6084/m9.figshare.21262935.v1)
71. Werden LK, Averill C, Crowther TW, Calderón-Morales E, Toro L, Alvarado JP, Gutiérrez LM, Mallory DE, Powers JS. 2022 Below-ground traits mediate tree survival in a tropical dry forest restoration. Figshare. (doi:10.6084/m9.figshare.c.6248839)