Using large-scale tropical dry forest restoration to test successional theory

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Abstract. Microclimatic conditions change dramatically as forests age and impose strong filters on community assembly during succession. Light availability is the most limiting environmental factor in tropical wet forest succession; by contrast, water availability is predicted to strongly influence tropical dry forest (TDF) successional dynamics. While mechanisms underlying TDF successional trajectories are not well understood, observational studies have demonstrated that TDF communities transition from being dominated by species with conservative traits to species with acquisitive traits, the opposite of tropical wet forest. Determining how functional traits predict TDF tree species' responses to changing environmental conditions could elucidate mechanisms underlying tree performance during TDF succession. We implemented a 6-ha restoration experiment on a degraded Vertisol in Costa Rica to determine (1) how TDF tree species with different resource-use strategies performed along a successional gradient and (2) how ecophysiological functional traits correlated with tree performance in simulated successional stages. We used two management treatments to simulate distinct successional stages including: clearing all remnant vegetation (early-succession), or interplanting seedlings with no clearing (mid-succession). We crossed these two management treatments (cleared/interplanted) with two species mixes with different resource-use strategies (acquisitive/conservative) to examine their interaction. Overall seedling survival after 2 yr was low, 15.1–26.4% in the four resource-use-strategy × management-treatment combinations, and did not differ between the management treatments or resource-use-strategy groups. However, seedling growth rates were dramatically higher for all species in the cleared treatment (year 1, 69.1% higher; year 2, 143.3% higher) and defined resource-use strategies had some capacity to explain seedling performance. Overall, ecophysiological traits were better predictors of species' growth and survival than resource-use strategies defined by leaf and stem traits such as specific leaf area. Moreover, ecophysiological traits related to water use had a stronger influence on seedling performance in the cleared, early-successional treatment, indicating that the influence of microclimatic conditions on tree survival and growth shifts predictably during TDF succession. Our findings suggest that ecophysiological traits should be explicitly considered to understand shifts in TDF functional composition during succession and that using these traits to design species mixes could greatly improve TDF restoration outcomes.

Key words: abiotic conditions; active restoration; community assembly; Costa Rica; degraded Vertisol; ecophysiology; microclimate; plant functional traits; resource-use strategies; succession.

Introduction

Regenerating secondary forests are now dominant globally (FAO 2015) and much effort has been devoted

to understanding the drivers of forest regeneration across the tropics (Chazdon 2014). A complex interplay between predictable and unpredictable factors leads to shifts in vegetation structure during tropical forest succession (Chazdon 2008). Deterministic factors that affect the rate and dynamics of succession include abiotic resources such as light and water availability, in addition to microclimatic conditions such as air and soil temperature (Loik and Holl 2001). These abiotic environmental factors change over the course of secondary

forest regeneration (Lebrija-Trejos et al. 2011), in turn affecting biogeochemical cycles and ecosystem processes such as carbon storage and fluxes (Powers and Marín-Spiotta 2017). Because microclimatic conditions (e.g., light and water availability) can change dramatically as a forest ages and its canopy develops (Lebrija-Trejos et al. 2011), these conditions are strong filters of species assembly during tropical forest succession (Lebrija-Trejos et al. 2011, Lohbeck et al. 2013, Buzzard et al. 2016). Furthermore, morphological and physiological strategies of tree species follow predictable patterns as microclimate changes during succession; consequently, as forests age, trees face shifting limitations in resources such as light and water (Bazzaz and Pickett 1980, Montgomery and Chazdon 2002).

It is well established that light availability is the most limiting environmental factor in tropical wet forest succession, contributing to a transition from fast-growing, light-demanding species to slow-growing, shade-tolerant species (Bazzaz and Pickett 1980, Guariguata and Ostertag 2001, Montgomery and Chazdon 2002, Boukili and Chazdon 2017). By contrast, hypothesized amelioration of harsh microclimatic conditions as TDFs mature has led to the prediction that water availability may more strongly influence TDF successional processes than gradients in light availability (Lebrija-Trejos et al. 2010, Lebrija-Trejos et al. 2011, Lohbeck et al. 2013, Pineda-Garcia et al. 2013, Derroire et al. 2018). In theory, TDF species that are able to cope with low soil moisture and/or high temperatures and vapor pressure deficits should be dominant at earlier TDF successional stages (Lohbeck et al. 2013). Therefore, changes in microclimatic conditions during succession may play a major role in structuring TDF plant communities (Lebrija-Trejos et al. 2011, Jackson et al. 2018). Determining how species' resource-use traits mediate responses to shifts in abiotic gradients may clarify the mechanisms underlying TDF plant community assembly, which are currently not well understood (Quesada et al. 2009).

It has been argued that all plant species fall somewhere on a "fast-slow" plant economics spectrum, and species tolerant of drought and high temperatures fall on the slow, or conservative, end of the spectrum (Reich 2014). In this framework, acquisitive species maximize resource capture and are more sensitive to abiotic stress, while conservative species use resources more efficiently and are more stress-tolerant. Aligning with this expectation, some observational studies have shown that during succession TDF communities transition from being dominated by species with conservative leaf traits (e.g., smaller, thicker leaves) to species with acquisitive traits (e.g., larger, thinner leaves), both for adult trees (Becknell and Powers 2014, Buzzard et al. 2016) and saplings (Derroire et al. 2018), but some show the opposite trend (Lohbeck et al. 2013, Subedi et al. 2019). Similar patterns have been observed for some stem traits, with TDF tree communities shifting from having conservative (dense) to acquisitive (soft) wood density values over time (Lohbeck

et al. 2013, Poorter et al. 2019, but see Subedi et al. 2019). Generally, these studies argue that TDF community assembly patterns are driven by water limitation at early-successional stages, leading to the dominance of species with conservative resource-use strategies (drought and temperature tolerant) in early-successional environments such as completely cleared pastures, eventually transitioning to dominance by species with acquisitive strategies (more profligate resource-use, less stress-tolerant; Lebrija-Trejos et al. 2010, Lohbeck et al. 2013). While studies have demonstrated how TDF functional composition shifts over time, the mechanisms underlying how species-level resource-use strategies dictate performance (i.e., survival and growth) during succession have not been explicitly investigated. Active restoration experiments provide excellent opportunities to test these theories experimentally (Howe and Martínez-Garza 2014), while simultaneously promoting regrowth of the critically endangered TDF biome (Janzen 1988).

We implemented a 6-ha TDF restoration experiment in northwestern Costa Rica to test how tree species with differing resource-use strategies (acquisitive or conservative) respond when planted into TDF successional stages with differing microclimatic conditions. We used two management treatments to simulate two distinct successional stages including: clearing all remnant vegetation to mimic early-successional environments (cleared treatment), or interplanting seedlings into plots with minimal site preparation to reflect a later, mid-successional environment (interplanted treatment). The goals of our experiment were to determine (1) how TDF tree species with different resource-use strategies perform in the presence or absence of remnant vegetation and (2) how ecophysiological (water-use and photosynthetic) functional traits correlate with tree performance in these simulated successional stages.

For our first goal, based on recent findings in secondary TDFs (Lohbeck et al. 2013, Buzzard et al. 2016, Derroire et al. 2018), we hypothesized that species with conservative trait syndromes would have higher performance (survival and growth rates) than acquisitive species when planted into an early-successional stage (lower water availability). This expectation was based on the understanding that conservative species are generally more tolerant of drought and temperature stress, enabled by strategies such as low specific leaf area and higher water-use efficiency (Niinemets 2001). By contrast, we hypothesized species with acquisitive trait syndromes would have higher performance than conservative species in a mid-successional stage (higher water availability) because they would be released from water limitation. Thus, we expected an interaction between trait syndromes and successional stage. Furthermore, there is growing evidence that water-use and photosynthetic traits, hereafter referred to as ecophysiological traits, are better predictors of species performance in regenerating tropical wet (Guimarães et al. 2018) and dry forests (Werden et al. 2018b) than easy to

measure "soft" leaf and stem traits. Consequentially, for our second goal we hypothesized that ecophysiological functional traits related to species' abilities to tolerate drought conditions in Vertisols (Werden et al. 2018b), soils with characteristic shrink-swell cycles (Deckers et al. 2001), would be stronger predictors of seedling performance than resource-use strategies defined with leaf and stem traits commonly used to examine shifts in functional composition during tropical forest succession. Additionally, we expected the strength of the relationships between species performance and ecophysiological traits would be stronger in the cleared than the interplanted treatment, due to amelioration of abiotic conditions by remnant vegetation as succession progresses (Lebrija-Trejos et al. 2011).

MATERIALS AND METHODS

Study site

We conducted our experiment from 2015 to 2017 at Estación Experimental Forestal Horizontes (10.712° N, 85.594° W), part of Área de Conservación Guanacaste in northwestern Costa Rica. The mean annual precipitation in this region is 1,730 mm, typically with a 5–6 month dry season with little to no rain (December or January–May; *data available online*).[8] In 2015, this region of Costa Rica experienced the strongest drought on record (Instituto Meterológico Nacional de Costa Rica 2015) and a meteorological station 1 km from our site recorded only 807 mm of precipitation for the year (53% lower than annual mean). The timing of precipitation in 2015 was irregular as well; wet season rains began in June but little rain fell in July and August, before consistent precipitation began in early September. Total precipitation in 2016 was 1754 mm (very close to the mean) and followed typical timing patterns (consistent precipitation June–November). The experiment was conducted on degraded Vertisols, soils that impede regeneration of large areas of TDF and are particularly difficult to restore because of low seedling survival rates (Werden et al. 2018b). The study site was previously used for cattle grazing, likely for decades, similar to other TDFs in this region (Janzen 1988) and across Central America (Griscom and Ashton 2011). Naturally regenerating vegetation at the site was in a state of arrested succession following abandonment for ~30 yr, which is typical for TDF on Vertisols in this region (M. Gutiérrez, *personal observation*).

Species selection and definition of resource-use strategies

We chose 12 focal species for plantings (Table 1), which commonly occur in TDFs in this region (Powers et al. 2009) and are able to persist on Vertisols (Werden et al. 2018b), with a range of resource-use and life

[8] https://www.acguanacaste.ac.cr/investigacion/datos-meterologicos

history functional traits (Powers and Tiffin 2010, Werden et al. 2018b). For these focal species, we used leaf and stem functional traits to define species' resource-use syndromes and to determine how ecophysiological traits explain species-level performance, thus allowing us to address our two primary study objectives (Table 2). To accomplish this we used a database of functional trait data collected in 2014 using standard methods (Pérez-Harguindeguy et al. 2013) for a previous study implemented at an adjacent site on the same soil type (Werden et al. 2018a, b). The functional trait data we used (Werden et al. 2018a, b) were collected 1 yr prior to the implementation of our restoration experiment in 2015, however, the environmental conditions experienced by seedlings were similar in both years due to an ongoing drought in the region (total precipitation 535 and 923 mm lower than average in 2014 and 2015, respectively). Additionally, all trait data were collected from seedlings grown in the same shade house where seedlings were produced for this experiment, or on seedlings planted <200 m from where this experiment was implemented. Because trait data from Werden et al. (2018a, b) were collected under similar environmental conditions, and in a location adjacent to our experiment, using these data in our experiment is unlikely to have influenced our results or conclusions.

From Werden et al. (2018b), we used the following traits commonly used to define resource-use strategies of tropical tree species (Goal 1): leaf thickness (mm), LDMC (leaf dry matter content; g/g), petiole length (mm), SLA (specific leaf area; cm^2/g), wood density (g/cm^3), foliar nitrogen concentration (%; foliar N). We used the following ecophysiological traits to address Goal 2: g_s (stomatal conductance; $mmol \cdot m^{-2} \cdot s^{-1}$), photosynthetic capacity (A_{max}; $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$), iWUE (instantaneous water-use efficiency; $\mu mol\ CO_2$/mmol H_2O), $\Delta\ \delta^{13}C$ (upregulation of integrated water-use efficiency; ‰). These ecophysiological traits were used to indicate how the focal species acquire carbon (A_{max}) and cope with water stress (iWUE, g_s, $\Delta\ \delta^{13}C$). For additional details on how functional trait data were collected, see Appendix S1: Section S1.

We defined acquisitive and conservative trait syndromes for the 12 focal species using six traits demonstrated to shift from conservative to acquisitive values during TDF succession (Lohbeck et al. 2013, Buzzard et al. 2016, Derroire et al. 2018; Goal 1 in Table 2). The 12 focal species were assigned to acquisitive or conservative groups using hierarchical cluster analysis (Appendix S1: Section S2, Figs. S1–S3). In the cluster analysis, we considered the six resource-use strategy leaf and stem traits (Goal 1; Table 2). This resulted in one resource acquisitive and one resource conservative group, with six species per group (Table 1). Consistent with general expectations of species with conservative resource-use strategies, species in the conservative group had lower SLA, thicker leaves, and lower foliar nitrogen concentrations. Petiole length, LDMC, and wood density did not differ between the acquisitive and

TABLE 1. Tropical dry forest species used in the experiment, grouped by resource-use strategies (acquisitive/conservative) and life history traits.

Genus species	Family	Leaf habit	Leaf type	Dispersal syndrome	Nitrogen fixer
Acquisitive group					
Acosmium panamense	Fabaceae	semi-deciduous	compound	wind	yes
Albizia saman	Fabaceae	semi-deciduous	compound	animal	yes
Dalbergia retusa	Fabaceae	deciduous	compound	wind	yes
Gliricidia sepium	Fabaceae	deciduous	compound	wind	yes
Lysiloma divaricatum	Fabaceae	deciduous	compound	wind	yes
Thouinidium decandrum	Sapindaceae	semi-deciduous	compound	wind	no
Conservative group					
Crescentia alata	Bignoniaceae	semi-deciduous	simple	animal	no
Hymenaea courbaril	Fabaceae	semi-deciduous	compound	animal	no
Pachira quinata	Malvaceae	deciduous	compound	wind	no
Rehdera trinervis	Verbenaceae	deciduous	simple	wind	no
Simarouba glauca	Simaroubaceae	evergreen	compound	animal	no
Tabebuia rosea	Bignoniaceae	deciduous	compound	wind	no

TABLE 2. Mean, minimum, maximum, and coefficient of variation (CV) of functional traits of the 12 tropical dry forest tree species planted in the restoration experiment.

Functional trait	Mean	Minimum	Maximum	CV (%)
Resource-use strategy traits (Goal 1)				
Petiole length (mm)	31.01	2.40	77.80	72.52
Leaf thickness (mm)	0.13	0.08	0.26	33.57
LDMC (g/g)	0.29	0.12	0.47	33.48
SLA (cm^2/g)	101.42	53.22	177.17	34.75
Wood density (g/cm^3)	0.66	0.38	0.84	24.97
Foliar N (%)	3.24	2.34	5.11	25.61
Ecophysiological traits (Goal 2)				
g_s ($mmol \cdot m^{-2} \cdot s^{-1}$)	619.89	97.97	1446.90	65.69
A_{max} ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	12.65	4.17	19.91	46.20
iWUE ($\mu mol\ CO_2$/mmol H_2O)	3.72	2.05	5.17	29.20
$\Delta\ \delta^{13}C$ (‰)	2.07	1.44	3.65	34.70

Notes: The six traits used to assign acquisitive or conservative resource-use strategies for each focal species using cluster analysis for Goal 1 (Appendix S1: Section S2) are at the top of the table. Ecophysiological traits used as predictors of seedling performance in Goal 2 are at the bottom of the table. LDMC, leaf dry matter content; SLA, specific leaf area; g_s, stomatal conductance; A_{max}, photosynthetic capacity; iWUE, instantaneous water-use efficiency; see Werden et al. (2018b) for more details on $\Delta\ \delta^{13}C$ measurements (upregulation of integrated water-use efficiency).

conservative groups (Appendix S1: Section S2). For more details on the methods used to define resource-use strategy groups, including functional traits means for each group, see Appendix S1: Section S2.

Plantation design and preparation

We crossed two management treatments (cleared/interplanted) with two resource-use strategy species mixes (acquisitive/conservative) to test for their interaction. We randomly assigned treatments to six 100 × 100 m plots, for a total of three interplanted plots and three cleared plots (Fig. 1). In June 2015, for the cleared treatment, we obtained necessary permits and fully cleared remnant vegetation with chainsaws and a tractor (Fig. 2). For the interplanted treatment we cleared narrow (~1 m wide) 100 m long planting rows 4 × 4 m apart with machetes. This enabled us to plant seedlings in orderly rows with minimal disturbance to remnant vegetation. Following site preparation, each 1-ha plot was divided into four 50 × 50 m split plots, and two replicates of each species mix (acquisitive/conservative) were randomly assigned to be planted in two split plots per plot (two replicate split plots per species mix × two split plots per plot × 6 plots = 24 split plots; 10 m gap between split plots; Fig. 1).

Remnant vegetation, fine root stocks, and microclimatic conditions in the treatments

In July 2016, we characterized remnant vegetation in the three interplanted treatment plots by measuring the DBH (diameter at breast height) of all trees ≥10 cm and identifying all trees to species. For multi-stemmed trees, we measured all stems ≥10 cm in DBH for each individual. We quantified fine root stocks in the six treatment plots in February 2018 as a proxy for belowground competition. We collected six root samples with a root corer (8 cm diameter, 15 cm depth) along two parallel transects (50 m apart) in each plot (6 plots × 2 transects per plot × 6 samples per transect = 72 root samples). We washed soil from roots, dried roots to constant mass at 60°C, and determined root dry mass (g) for each sample.

To characterize differences in microclimatic conditions between the cleared and interplanted treatments, we measured air/soil temperature and soil moisture during seasonal drought conditions and after the onset of the 2015 wet season. At the center of each plot, we used iButtons
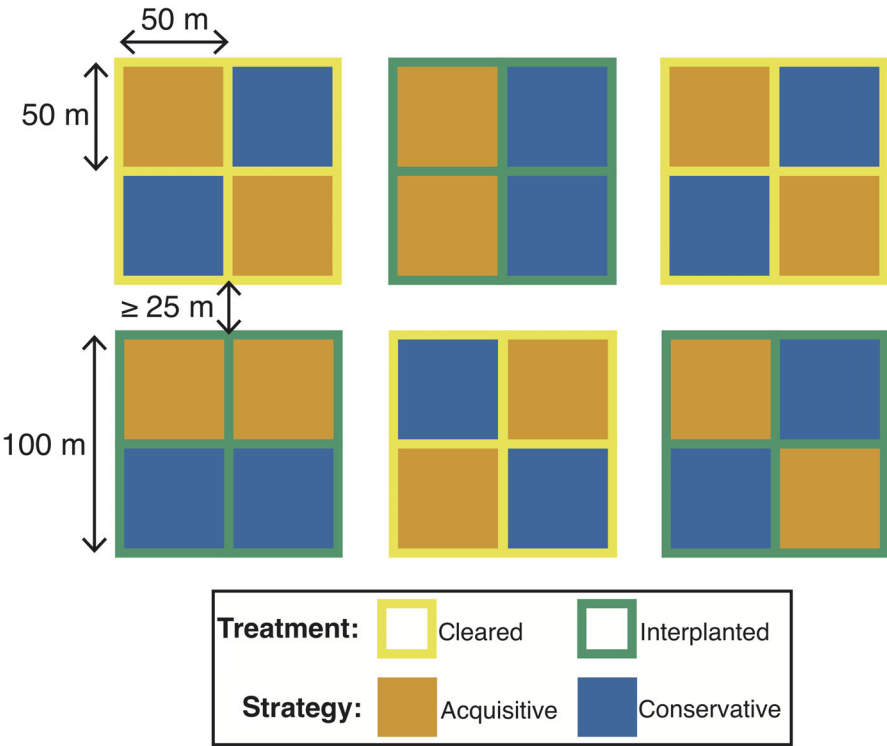
FIG. 1. Diagram of the 6-ha tropical dry forest restoration experiment implemented on degraded Vertisol soils. Management treatments (cleared/interplanted) were randomly applied to each 1-ha whole plot and resource-use strategy species mixes (conservative/acquisitive) were randomly applied to four split plots (0.25 ha; 10-m gap between split plots) within whole plots. A modified version of this figure is available in grayscale (Appendix S1: Fig. S6).

FIG. 2. Management treatments in the tropical dry forest restoration in the wet season. The photo on the left shows a cleared treatment plot (early-successional stage). The photo on the right shows an interplanted treatment plot (mid-successional stage).

(DS1921G-F5# Thermochron; Maxim Integrated, San Jose, California, USA) to simultaneously measure air temperature (0.5 m off the ground), and soil temperature (5 cm depth), for 10 d in August and 10 d in September 2015 to account for day-to-day variation in midday temperatures. Measuring over this period captured the transition from dry to wet conditions for this year. Before deployed in the field, all iButtons were checked to ensure measurements were internally consistent. We measured volumetric soil moisture (%) in the top 0–5 cm of the mineral layer with a soil moisture sensor (DeltaSM150, Delta-T Devices, Burwell, UK) three times: before we planted the experiment (during significant drought when almost no rain had fallen for two months; August 2015), after the onset of wet season rains (September 2015), and at the start of the wet season during the second year of the experiment (July 2016). We measured soil moisture every 5 m ($n = 20$ per transect) along three 100-m transects in each plot (center of plot and two transects equidistant from plot center in opposite directions). No precipitation fell during soil moisture measurements; thus, plot-to-plot measurements were comparable. Finally, in November 2017, when the canopy was fully leafed out, we quantified full-sun photosynthetically active radiation (PAR) at 1.5 m above the ground with an AccuPAR LP-80 Ceptometer (Decagon Devices, Washington, DC, USA), every 5 m along a transect down each plot center on a cloudless day ($n = 20$ per plot).

Seedling production, planting, and maintenance

We collected seeds and produced seedlings using local best-practice methods (Appendix S1: Section S3). In mid-September 2015, after the start of consistent wet season rains, we pre-dug holes in 4 × 4 m spacing in all six 1-ha plots. Two replicates each of the species mixes (acquisitive/conservative) were planted into the four 0.25-ha split plots at 4 × 4 m planting density (576 seedlings/ha; 3,456 seedlings total) over 10 d in September 2015. We planted seedlings (height: mean, 22.6 cm, minimum, 2.4 cm, maximum, 87 cm; σ = 14.8) in each split plot using a multiple Latin-square design following Potvin and Dutilleul (2009), where species were planted in the same sequence with each species occurring twice in each row, to have the ability to examine neighborhood effects in the future. All seedlings were planted with soil amendments that aided first-year establishment on Vertisols in this region (Appendix S1: Section S3; Werden et al. 2018b). To minimize competition with non-native pasture grasses, grasses were cleared from the base of seedlings with machetes three times in both the interplanted and cleared treatments (December 2015, June 2016, May 2017).

Seedling survival and growth measurements

We measured seedling survival and growth for two years (two full wet and dry seasons). During each survey, we determined survival and measured the height (at the apical meristem) of all planted seedlings. Seedlings were assumed to be dead if they lacked leaves and had a completely dry stem. Surveys were conducted after planting (September 2015) to obtain initial height and survival measurements (post-transplant shock), at the end of the first wet (growing) season (December 2015) and at the end of both dry seasons (July 2016 and May 2017). A previous study at this site found minimal seedling mortality during the second wet season, and minimal growth during the second dry season (Werden et al. 2018b), therefore no survey was conducted after the second wet season.

Statistical analysis

We tested for seasonal differences in soil moisture, soil temperature, and air temperature between management treatments using Tukey's HSD post hoc tests performed on one-way ANOVAs, with microclimatic variables as the responses and management treatment as the predictor. We used the same method to test for differences in PAR between the management treatments in November 2017. To characterize remnant vegetation in the interplanted treatment we calculated the total number of stems and basal area (m^2/ha) for each treatment plot. We estimated "effective" stand age of the three interplanted plots by comparing the total basal area of trees in these plots to 84 chronosequence plots of naturally regenerating TDF in the same region (Powers et al. 2009, Becknell and Powers 2014). We compared the microclimatic data we collected to air temperature (Derroire et al. 2018) and PAR data (J. S. Powers, *unpublished data*) collected in 12 of the chronosequence plots. This allowed us to determine the extent to which the interplanted treatment resembled early- or mid-successional stages from the perspective of basal area and microclimatic conditions.

To quantify the performance of TDF seedlings with differing resource-use strategies at early and mid-successional stages (management treatments; Goal 1) we used individual seedling growth and survival measurements over two years. First, we calculated absolute height growth rates (AGR; cm/d) for each year for individual seedlings with the standard AGR equation (height$_{final}$ − height$_{initial}$) − (day$_{final}$ − day$_{initial}$). Following these calculations, we fit mixed effects models to quantify the effects of management treatments and species' resource-use strategies on seedling survival and AGR. For survival, we fit a mixed effects multiple logistic regression model with seedling survival at the end of the experiment as the response, and management treatment (treatment), resource-use strategy (strategy), and the interaction between treatment and strategy (treatment × strategy) as fixed effect predictors (Appendix S1: Table S1; lme4 package in R). The natural logarithm (ln) of initial seedling height was included as a covariate. Variation in micro-topography and other environmental factors was controlled for by including the 0.25-ha split plots nested under the 1-ha whole plots as a

random effect. Species was included as a random effect to account for species-level variation.

For AGR, we fit a mixed-effects multiple linear regression model with seedling AGR as the response (square root-transformed to meet normality assumptions). The same fixed effect predictors (strategy and treatment) were included with the addition of year as a predictor, to consider the effects of the drought (2015; 807 mm) and average precipitation (2016; 1,754 mm) years on seedling AGR. All two-way interactions and the three-way interaction of the predictors were also included. The same covariate and random effects as the survival model were used in the AGR model (Appendix S1: Table S2). We removed seedlings with negative growth rates, resulting from the top of the stem dying, from the model ($n = 104$). This allowed us to obtain better estimates of mean AGR, but did not affect the overall significance of model terms. The marginal (fixed effects; R_m^2) and conditional (fixed and random effects; R_c^2) R^2 values for all models were obtained (Nakagawa et al. 2017; MuMIn package in R). Interclass correlation coefficients were computed for the survival and AGR models to determine the proportion of variance explained by the random effects (Hox 2002; sjstats package in R). For the survival and AGR models, we used likelihood ratio (LR) chi-squared (χ^2) tests to determine the significance of fixed effect model terms. For significant model terms we used pairwise comparisons (Tukey corrected) of estimated least-square means to test for differences in seedling AGR between management treatments, and for differences in AGR between the resource-use strategy groups within management treatments (emmeans package in R).

Last, to determine if ecophysiological traits explained species performance across simulated successional stages (Goal 2), we fit the same mixed effects models described above, this time with four individual ecophysiological traits instead of resource-use strategy as predictors of survival and AGR, again using individual seedlings as an observation (Table 3). We fit the same models using the six individual traits used to define resource-use strategies as predictors to have the ability to directly compare the predictive power of individual ecophysiological traits to individual leaf and stem traits (Table 3). Before fitting models, we performed a z-transformation to standardize all traits values, so the effect sizes from each model (standardized regression coefficients; β_{std}) could be directly compared, by subtracting the trait mean from each species-level trait value then dividing by the standard deviation.

We then fit 10 models total for each response variable (four ecophysiological traits and six leaf and stem traits; Table 3), one for each trait in place of resource-use strategy as a predictor (e.g., abbreviated survival model: survival ~ treatment × trait + ln(initial height) + random effects; abbreviated AGR model: √AGR ~ treatment × trait × year + ln(initial height) + random effects). For each response variable, we also fit a null model including all predictors except the individual traits (e.g., abbreviated survival null model: survival ~ treatment + ln(initial height) + random effects; abbreviated AGR null model: √AGR ~ treatment × year + ln(initial height) + random effects) to determine if including the traits improved fits. We computed variance inflation factors for predictors and verified that collinearity did not affect regression estimates (car package in R). The null model, the individual trait models, and the resource-use strategy model created for Goal 1, were ranked using the Akaike Information Criterion (AIC) for each response variable. Model averaging is not appropriate for this analysis because it is ineffective when evaluating models with interaction terms (Cade 2015). For each model, marginal and conditional R^2 values were determined and the β_{std} for each predictor extracted.

We tested for differences in the strength of relationships (slope) between traits and seedling performance (survival or AGR) in each management treatment for models with significant higher order interaction terms (i.e., treatment × trait for survival; treatment × trait × year for AGR) ranked higher than the resource-use strategy model (indicated by lower AIC scores). If the slope of performance × trait relationships differed between management treatments, we interpreted this as evidence that this trait had a differential effect on overall seedling performance between the cleared and interplanted treatments. A steeper performance × trait slope signified a trait had a stronger effect on seedling performance in the management treatment, or vice versa. No difference between slopes, i.e., approximately parallel lines, indicates the relationship between a trait and seedling performance did not differ by management treatment. We visualized those relationships with interaction plots produced by plotting the full models including all interaction terms (emmeans package in R). Intercepts of performance by trait relationships in these plots represent differences in mean AGR or survival probability between management treatments. All analyses were conducted in R version 3.5.1 (R Development Core Team 2018).

Results

Remnant vegetation and microclimatic conditions in the management treatments

The interplanted treatment was dominated by three tree species that accounted for 85% and 86% of stems and basal area, respectively (see Appendix S1: Section S4 for more on remnant vegetation). The basal area of trees in the interplanted treatment plots ranged from 2.43 to 4.91 m²/ha (±0.73 SE). Stands with basal area in this range generally have ~5–10 yr of regrowth (Powers et al. 2009, Becknell and Powers 2014). Thus, while the interplanted stands have ~30 yr of regeneration, they resemble early-successional forest on more amenable soils in

TABLE 3. Mixed-effects model comparisons substituting ecophysiological traits (boldface), or leaf and stem traits, for resource-use strategy (italicized).

Trait	AIC	R^2_m	R^2_c	Treatment	Trait	Year	log(initial height)	Treatment × Trait	Treatment × Year	Trait × year	Treatment × trait × year
(a) Seedling survival											
A_{max}	2284	0.22	0.43	ns	1.22***		0.62***	ns			
iWUE	2285	0.17	0.44	ns	1.13***		0.59***	−0.34**			
g_s	2734	0.13	0.42	ns	0.89**		0.67***	ns			
$\Delta \delta^{13}C$	2735	0.05	0.42	ns	ns		0.61***	0.21**			
Petiole length	2736	0.17	0.43	ns	−0.94**		0.65***	ns			
Leaf thickness	2737	0.04	0.43	ns	ns		0.61***	ns			
No trait	2738	0.03	0.43	ns	—		0.63***	—			
SLA	2738	0.04	0.42	ns	ns		0.62***	ns			
Strategy	2739	0.04	0.42	ns	ns		0.63***	ns			
Wood density	2740	0.05	0.43	ns	ns		0.62***	ns			
LDMC	2740	0.03	0.42	ns	ns		0.63***	ns			
Leaf N	2740	0.05	0.42	ns	ns		0.65***	ns			
(b) Seedling AGR (square root-transformed)											
$\Delta \delta^{13}C$	−2138	0.18	0.46	−0.06***	ns	0.11***	ns	ns	−0.08***	−0.05***	0.04***
g_s	−2121	0.28	0.47	−0.05***	0.05*	0.08***	ns	−0.02*	−0.06***	0.03***	−0.03*
Leaf N	−2118	0.16	0.46	−0.06***	ns	0.09***	ns	ns	−0.06***	−0.02**	0.06***
Strategy	−2118	0.17	0.46	−0.04***	ns	0.10***	ns	ns	ns	ns	−0.08***
SLA	−2113	0.18	0.45	−0.06***	ns	0.09***	ns	0.02**	−0.07***	ns	ns
LDMC	−2105	0.2	0.44	−0.06***	ns	0.09***	ns	0.02***	−0.07***	ns	ns
Petiole length	−2100	0.16	0.44	−0.05***	ns	0.11***	ns	ns	−0.08***	0.05***	ns
Leaf thickness	−2094	0.15	0.45	−0.06***	ns	0.09***	ns	ns	−0.07***	ns	−0.04*
Wood density	−2092	0.15	0.44	−0.06***	ns	0.09***	ns	ns	−0.08***	ns	ns
No trait	−2090	0.15	0.38	−0.06***	—	0.09***	ns	—	−0.07***	—	—
iWUE	−1784	0.28	0.43	−0.06***	0.08**	0.10***	ns	ns	−0.10***	−0.04**	0.05*
A_{max}	−1780	0.27	0.44	−0.05***	0.07**	0.09***	ns	−0.02*	−0.10***	−0.03*	0.04*

Notes: These models were fit to demonstrate how these traits affect (a) tropical dry forest seedling survival and (b) absolute growth rate (AGR). Results from a null model including all predictors except an individual trait is labeled "no trait." (a) Results of logistic regression results with seedling survival as the response and treatment, trait, and interaction of the two as predictors and (b) linear regression results with AGR as the response and treatment, trait, year, and two-way/three-way interactions as predictors. All models include the natural logarithm of initial seedling height as a covariate, and species and split plots nested under whole plots as random effects. Models were ranked with Akaike Information Criterion (AIC). Standardized effect size (β_{std}) for each predictor and the variance explained by fixed (R^2_m) and fixed and random effects (R^2_c) are reported. Likelihood ratio and chi-squared tests were used determine the significance of fixed effect model terms. Dashes indicate terms not present in the model, asterisks indicate significance of predictors (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$), and ns indicates not significant.

the region. Fine root stocks were 60.6% lower in the cleared than the interplanted treatment on average, indicating that management existing vegetation reduced fine root stocks after two years ($n = 72$, $t = -5.63$, $P < 0.001$; Fig. 3a).

Microclimatic conditions differed significantly between the management treatments; compared to the cleared treatment, the interplanted treatment received only 17.6% of total incoming PAR ($n = 120$, $t = -8.82$, $P < 0.001$; Fig. 3b), and had 2.1°C lower midday air ($n = 60$, $t = -5.7$, $P < 0.001$; Fig. 3c) and 3.7°C lower soil temperatures during the wet season ($n = 60$, $t = -8.0$, $P < 0.001$; Fig. 3d). Differences in soil moisture between the management treatments were very modest (~2–5%), and the relative rank of differences switched from the dry to the wet season. During dry conditions (August 2015), soil moisture was 3.3% higher in the interplanted treatment ($n = 360$, $t = 16.0$, $P < 0.001$), but in the wet-season (September 2015), soil moisture was 5.0% higher in the cleared treatment ($n = 360$, $t = -5.2$, $P < 0.001$; Fig. 3e). Differences in wet-season soil moisture between the treatments remained consistent over time as soil moisture in the wet season of the second year of the experiment (July 2016) was 2.0% higher in the cleared treatment ($n = 360$, $-t = 6.27$, $P < 0.001$; Appendix S1: Fig. S4). Furthermore, an ongoing study of TDF microclimate at a nearby site has showed that open field Vertisol sites have lower soil moisture than forested sites at the peak of the dry-season (J. Tijerin, *personal communication*), consistent with our observation that dry-season soil moisture was lower in the open field cleared treatment than in the interplanted treatment. Overall, these results indicate that the interplanted treatment represents a mid-successional stage (≥ 30 yr old) in terms of light availability (PAR) and air temperature when compared to a TDF chronosequence in the same region (see Appendix S1: Section S4).

Seedling survival and growth after two years

Overall seedling survival after two years ranged from 15.1% for acquisitive species in the cleared treatment to 26.4% for conservative species in the cleared treatment (Appendix S1: Fig. S5; see Appendix S1: Table S3 for survival by species). Likely attributed to the severe drought in year 1, three acquisitive (*Acosmium panamense*, *Albizia saman*, *Thouinidium decandrum*) and one conservative species (*Pachira quinata*) had no surviving individuals in either management treatment by the end of the experiment (Appendix S1: Table S3). There were no significant differences in survival among management treatments or resource-use strategies (Fig. 4a), and management treatments and resource-use strategies explained little variation in seedling survival after two years ($R_m^2 = 0.04$). By contrast, species and split plot level effects explained a majority of variation ($R_c^2 = 0.42$), with species explaining 70% of variation in the random effects. Furthermore, overall species composition of surviving individuals did not differ between the management treatments at the end of the experiment, i.e., results were not driven by intra-specific differences in survival between treatments (Appendix S1: Table S3). The only significant predictor of survival after two years was seedling height at planting ($\chi^2_{df=1} = 22.60$, $P < 0.001$; Appendix S1: Table S1).

For seedling growth, management treatment was a significant predictor of AGR ($\chi^2_{df=11} = 14.44$, $P < 0.001$; Appendix S1: Table S2). Independent of resource-use strategy, seedlings had dramatically higher AGR in the cleared than the interplanted treatment in both years (Fig. 4b; year 1, cleared 69.1% higher, $t = 7.29$, $P < 0.001$; year 2, cleared 143.4% higher, $t = 11.34$, $P < 0.001$). A three-way interaction between management treatment, resource-use strategy, and year ($\chi^2_{df=1} = 10.28$, $P < 0.001$; Appendix S1: Table S2) was driven by conservative species having 66.8% lower AGR than acquisitive in the interplanted treatment in year 2 ($t = 3.90$, $P < 0.001$) under average precipitation. When compared to the survival model, the fixed-effects predictors explained more variation in AGR ($R_m^2 = 0.17$). However, the random effects still explained a majority of variation in seedling AGR ($R_c^2 = 0.46$), with species explaining 98% of variance in the random effects.

Ecophysiological functional traits as predictors of survival and growth

The series of models we fit demonstrated that ecophysiological functional traits were better predictors of seedling survival and growth than the conservative and acquisitive resource-use strategies defined by "soft" leaf and stem traits (Table 3). Here we present results for the models ranked higher with AIC than the resource-use strategy model. For seedling survival, all candidate models were ranked higher than the resource-use strategy model (Table 3a). The best model for survival included A_{max} as a predictor and improved the variance explained considerably over the resource-use strategy model ($R_m^2 = 0.22$ for A_{max} model, $R_m^2 = 0.04$ for strategy model; Table 3). A null model including only a covariate for initial height and the random effect terms as predictors of survival had a modest improvement (AIC = 2,738) over the resource-use strategy model (AIC = 2,739); further evidence that resource-use strategy was a poor predictor of survival.

Higher rates of A_{max} (photosynthetic capacity; $\beta_{std} = 1.22$, $P < 0.001$), iWUE (instantaneous water-use efficiency; $\beta_{std} = 1.13$, $P < 0.001$), and g_s (stomatal conductance; $\beta_{std} = 0.89$, $P = 0.01$) were all positively associated with higher seedling survival. Petiole length was the only leaf trait associated with survival ($\beta_{std} = -0.94$, $P = 0.007$), indicating that species with shorter petioles had higher survival, though all ecophysiological traits were ranked higher (Table 3a). Additionally, species-level iWUE and Δ $\delta^{13}C$ (the capacity of a species to upregulate integrated water-use efficiently after planted
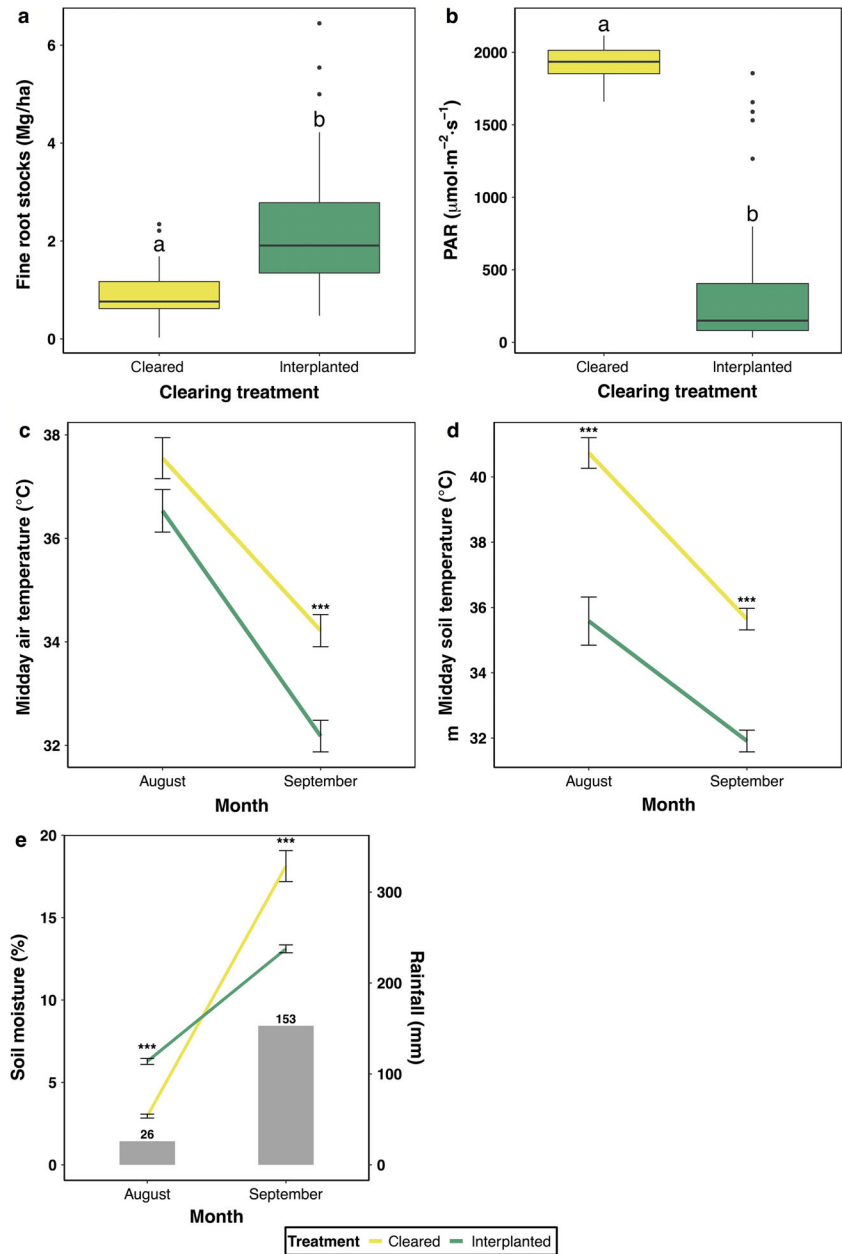
FIG. 3. (a) Fine root stocks, (b) photosynthetically active radiation (PAR), (c) midday air and (d) soil temperature, and (e) soil moisture in the tropical dry forest restoration management treatments (cleared/interplanted). In panels a and b, the center line is the median, the top and bottom of each box are upper and lower quantiles, and letters indicate significant differences between treatments (paired *t* tests). In panels c and e, error bars are standard errors of the mean and differences between treatments are indicated by ***$P < 0.001$ (paired *t* tests). In panel e, lines show soil moisture and gray bars indicate monthly rainfall.

from nursery to field; see Werden et al. 2018*b*) interacted significantly with management treatment, indicating that these traits had a stronger effect on survival (steeper slope) in the cleared treatment (iWUE, Fig. 5a, 62% larger effect, $z = 3.04$, $P = 0.002$; $\delta^{13}C$, Fig. 5b, 83% larger effect, $z = 2.46$, $P = 0.01$). For seedling AGR, only three models were ranked higher than the resource-use strategy model (two ecophysiological traits: $\Delta\,\delta^{13}C$ and g_s

and one leaf trait: foliar nitrogen concentration; Table 3b). For the $\Delta\,\delta^{13}C$, g_s, and foliar nitrogen models, there was a significant three-way interaction among management treatment, trait, and year (Fig. 6). Interestingly, in year 2, seedlings with the highest $\Delta\,\delta^{13}C$ (Fig. 6a) and foliar nitrogen concentrations (Fig. 6c) had lower AGR in the cleared treatment. Furthermore, species with higher foliar nitrogen concentrations had higher AGR in
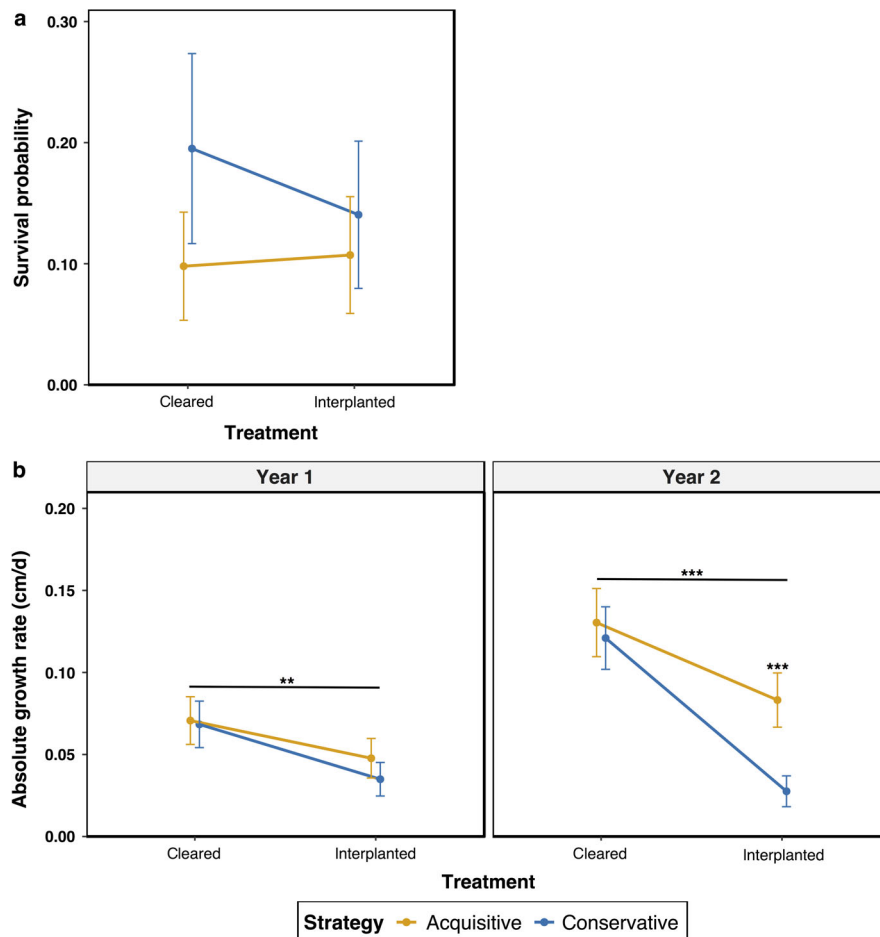
Fig. 4. (a) Survival probability of tropical dry forest seedlings in two resource-use strategy groups (conservative/acquisitive) planted into two management treatments (cleared/interplanted) estimated by mixed effects multiple logistic regression with ±SE bars (marginal R^2 = 0.04; conditional R^2 = 0.42). (b) Mean seedling absolute growth rates (back-transformed from square-root transformation) estimated by mixed effects multiple linear regression (marginal R^2 = 0.17; conditional R^2 = 0.46). Error bars are ±SE, horizontal bars with asterisks indicate significant differences between treatments independent of resource-use strategy, and asterisks above error bars indicate significant differences between resource-use strategies within a treatment (**P < 0.01, ***P < 0.001; pairwise tests with Tukey correction on least square means).

the interplanted treatment (Fig. 6c). Last, similar to findings for seedling survival, g_s was positively associated with seedling AGR (β_{std} = 0.05, P = 0.02), and the effect was stronger in the cleared treatment (Fig. 6a; year 1, 50% larger effect, t = 2.34, P = 0.02; year 2, 105% larger effect, t = 4.22, P < 0.001).

DISCUSSION

Our goals were to determine experimentally how TDF tree species with contrasting resource-use strategies defined with leaf and stem traits responded to changes in abiotic environmental conditions along a simulated successional gradient. Our results suggest large shifts in microclimate from early-successional (cleared) to mid-successional (interplanted) stages likely influenced seedling growth rates, but not survival, and that ecophysiological functional traits differentially influenced responses

between treatments. Binning species into resource-use strategies did not explain patterns in seedling survival; but, consistent with recent hypotheses about TDF successional theory (Lohbeck et al. 2013), acquisitive species had higher growth rates than conservative in the interplanted treatment. However, ecophysiological traits were always better predictors of survival than binary resource-use strategies, and two out of five ecophysiological traits were better predictors of seedling growth rates. As predicted, ecophysiological traits relating to water-use had stronger effects on survival and growth in the cleared treatment, indicating that the influence of water-use traits on plant performance decreases from early- to mid-successional stages in TDF. Our data allow us to quantify the extent to which management treatments affected seedling performance, how functional traits help explain responses, and how we can leverage this knowledge to design more effective TDF restorations.
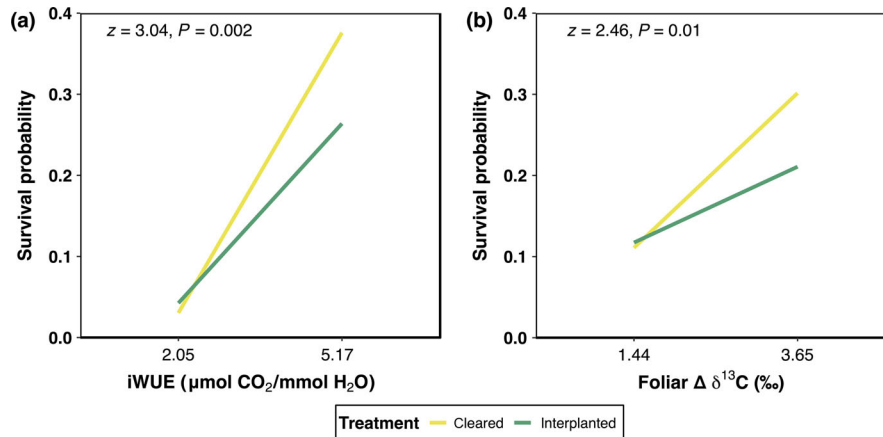
FIG. 5. Treatment × trait interaction plots for tropical dry forest seedling survival estimated by mixed models (Table 3a) for (a) instantaneous water-use efficiency (iWUE) and (b) foliar $\Delta \delta^{13}C$ (the ability to upregulate integrated water-use efficiency after outplanted; Werden et al. 2018b). The minimum and maximum values for traits are shown on the x-axis, and z and P values indicate significant differences in the slopes of survival by trait relationships between management treatments (cleared/interplanted).

Abiotic conditions in management treatments and their influence on overall survival and growth

After ~30 yr of regeneration, the basal area of remnant vegetation in the interplanted treatment was comparable to 5–10 yr of forest regrowth on other soil types in this region, underscoring that Vertisols soils present significant challenges for forest regeneration (Powers et al. 2009). However, from the perspective of microclimate, the abiotic conditions in the interplanted treatment resembled those in nearby mid-successional forest (Appendix S1: Section S4; Derroire et al. 2018) in terms of both light availability (Fig. 3b), and air and soil temperatures (Fig. 3c, d). Thus, from a structural perspective, while the interplanted treatment had low forest cover, what trees and shrubs were there clearly modified the abiotic conditions experienced by seedlings.

Interestingly, the relative ranks of soil moisture in the management treatments switched seasonally and the interplanted treatment had lower wet season soil moisture (Fig. 3e). While this contrasts strongly with patterns in other successional TDF (Lebrija-Trejos et al 2010), this result is largely consistent with additional observations from this site in Costa Rica and from Puerto Rico (J. Tijerin, *personal communication*). There are several potential mechanisms that may explain this pattern: first, higher vegetation density (e.g., basal area, fine root stocks) in the interplanted sites may result in higher transpiration rates (Ellison et al. 2017) and/or increased canopy interception (Jiménez-Rodríguez and Calvo-Alvarado 2014). Regardless of the mechanisms, contrary to our expectation that light would be higher in the cleared sites but wet season soil moisture would be higher in the interplanted sites, these data suggest that both soil moisture and light availability were higher in the cleared sites during the wet season (Figs. 3b, e). Because microclimate conditions play a central role in

our understanding of how shifts in abiotic conditions during succession influence TDF community assembly, this is a high priority area for additional studies.

Water limitation during the dry season typically has the largest impact on seedling survival on Vertisols (Werden et al. 2018b) and the cleared treatment exposed seedlings to the lowest mean soil moisture during the dry season (Fig. 3e). However, we did not observe differences in overall survival rates between the management treatments (Fig. 4a), implying that water availability at early- and mid-successional TDF stages may not differentially influence seedling survival in our system. However, we did observe that overall seedling growth rates were dramatically higher in the cleared treatment (Fig. 4b). This suggests that shifts in species dominance during TDF succession on Vertisols could instead be mediated by decreases in light availability (Fig. 3b) and/or increases in competition for belowground resources by fine roots (Fig. 3a), which can strongly limit seedling growth in this region (Gerhardt 1996), though we cannot tease apart the influence of these factors. Furthermore, our results may be influenced by the selection of species with high performance in drought conditions in a previous study (Werden et al. 2018b), and we may have selected 12 species, from a pool of 32, best adapted to tolerate drought in early-successional conditions. However, one-third of our focal species had no surviving individuals at the end of the experiment, suggesting that the species we planted were not all tolerant of severe drought conditions. Collectively, our results indicate that microclimate and competition may interact in a complex manner to influence TDF seedling growth. Nonetheless, while all species had higher growth in a simulated early-successional environment (cleared treatment), where there was high light and low belowground competition, these factors did not lead to differential survival between our management treatments.
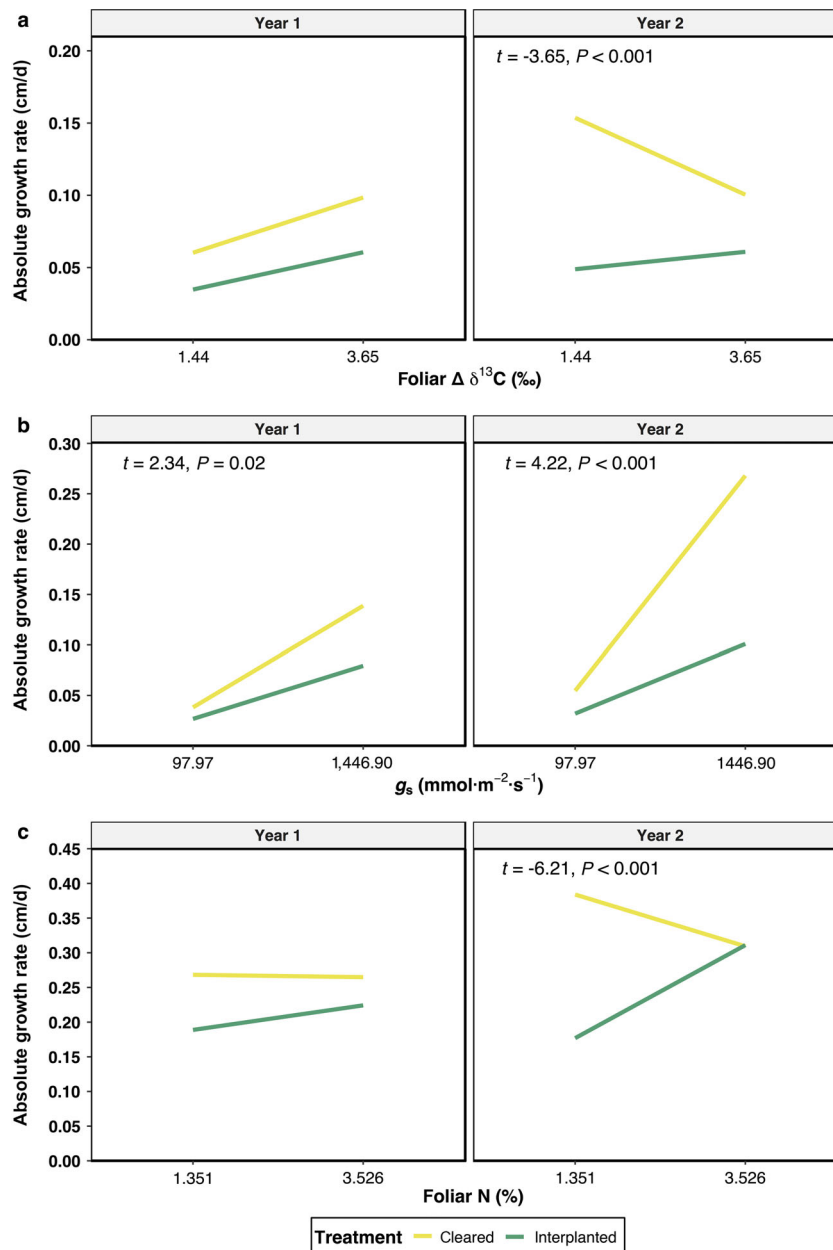
Fig. 6. Treatment × trait × year interaction plots for tropical dry forest seedling absolute growth rate (back-transformed from square root transformation) estimated from mixed models (Table 3b) for: (a) foliar Δ δ^{13}C (the ability to upregulate integrated water-use efficiency after planted; Werden et al. 2018b); (b) stomatal conductance (g_s); and (c) foliar nitrogen concentration (foliar N). The minimum and maximum values for traits are shown on the x-axis, and t and P values indicate significant differences in the slopes of growth by trait relationships between management treatments (cleared/interplanted).

Resource-use strategies and species performance

Although plants fall along a continuum of resource-use strategies (Wright et al. 2004), we were able to bin species into acquisitive and conservative groups (Table 1; Appendix S1: Fig. S1) using functional traits previously demonstrated to shift predictably during TDF succession (Lohbeck et al. 2013, Buzzard et al. 2016). Furthermore, our cluster analysis was robust to which species were included in it, as groupings were consistent when adding 15 additional commonly occurring tree species from the region (Appendix S1: Fig. S2). While these groupings followed general patterns expected of species with conservative or acquisitive strategies (Lohbeck et al. 2013, Buzzard et al. 2016), the acquisitive group appeared to have higher wood density than the conservative group (Appendix S1: Fig. S3), though the groups did not differ statistically ($P = 0.10$,

Appendix S1: Section S2). This was due to the high wood densities of nitrogen-fixing legumes in the acquisitive group (Appendix S1: Section S2, Fig. S3), a finding noted by other studies (Powers and Tiffin 2010). This highlights a potential pitfall of relying on the handful of quantitative leaf and stem traits typically used to assign resource-use strategies across wide tropical precipitation gradients, as the acquisitive group was dominated by nitrogen-fixing legumes (Table 1) usually favored in early- to mid-successional tropical forests (Batterman et al. 2013, Powers and Marín-Spiotta 2017), particularly in Neotropical TDFs (Gei et al. 2018). However, while higher seedling stem densities can confer increased drought tolerance (Poorter and Markesteijn 2008), we did not find evidence that this was the case for the acquisitive species group.

Acquisitive-conservative resource-use strategy groupings had some capacity to explain seedling responses, and the acquisitive group had higher mean AGR than the conservative in the interplanted treatment during a year with average rainfall (year 2; Fig. 4b). This result aligns with the recent hypothesis that acquisitive species should dominate in later-successional TDF (Lohbeck et al. 2013); however, this was the only instance where resource-use strategy groupings described patterns of seedling performance. The acquisitive-conservative groupings did not explain seedling survival (Fig. 4a), and a majority of variation in seedling responses in the management treatments was explained by interspecific differences in survival and growth (survival: 70% of variation; growth: 98% of variation). By contrast, ecophysiological traits explained both seedling survival and growth responses and were almost always stronger predictors of seedling performance than species' resource-use strategies.

Ecophysiological are strong predictors of seedling performance

Ecophysiological traits always improved predictions of seedling survival when compared to resource-use strategies defined with leaf and stem traits (Table 3a), and two out of five traits improved predictions of seedling growth (Δ δ^{13}C and g_{s}; Table 3b). Furthermore, while iWUE was not predictive of seedling growth in a disturbed tropical wet forest (Guimarães et al. 2018), we found iWUE to be positively associated with both seedling survival and growth, consistent with the understanding that water availability is a more important driver of species performance in systems with strong annual water limitation such as TDF (Pineda-Garcia et al. 2013). Individual leaf and stem traits used to define resource-use strategies were generally poor predictors of seedling performance, though one leaf trait was associated with survival (petiole length) and one was associated with growth (foliar nitrogen). Overall, these results confirm our hypothesis that ecophysiological traits are strong predictors of TDF seedling performance (Goal

2). We argue this is strong evidence that leaf and stem traits generally used to define resource-use strategies for tropical trees have limited capacity to categorize tree performance in early- to mid-successional TDF, consistent with recent work highlighting that commonly measured functional traits are poor predictors of tree demographic rates (Yang et al. 2018). We also emphasize the importance of considering ecophysiological traits when explaining patterns of early-successional TDF community assembly, although they are considerably more difficult to measure than "soft" traits such as SLA. Because "soft" leaf and stem traits are generally not correlated with ecophysiological traits of seedlings in this TDF (Werden et al. 2018b), it is especially important to focus future research on determining how community-level ecophysiological traits shift over TDF successional trajectories. Although ecophysiological traits were almost always better predictors of TDF seedling performance in our restoration experiment, some leaf traits were helpful in understanding how light availability influenced seedling responses, namely petiole length and foliar nitrogen.

Species with long petioles maximize light capture (Niinemets et al. 2004), placing them on the acquisitive end of the resource-use spectrum. We found that petiole length was negatively associated with survival rates (Table 3a), signifying that conservative values of this trait conferred a survival advantage across both clearing treatments. Foliar nitrogen, which is positively associated with photosynthetic rates (Poorter and Bongers 2006), was the only leaf trait predictive of seedling growth. This trait had a complex relationship with seedling performance: species with conservative (low) values of leaf nitrogen had higher growth rates in the cleared treatment and species with acquisitive (high values) of leaf nitrogen had higher performance in the interplanted treatment (Fig. 6c). This finding is consistent with the expectation that TDF communities transition from having conservative to acquisitive trait values. However, our observation that two leaf traits associated with species' light requirements (petiole length and foliar nitrogen) helped to explain seedling performance deserves further investigation especially because TDF community dynamics are generally assumed to be associated more with water availability. It will be important to tease apart how these abiotic environmental factors influence the magnitude of relationships between species' traits and performance.

Abiotic conditions have a stronger effect on plant performance at early-successional stages

Many studies have demonstrated that the functional composition of tropical forests can be driven by shifts in environmental conditions during succession (Lebrija-Trejos et al. 2010, Lohbeck et al. 2013, Boukili and Chazdon 2017), and that the relative influence of abiotic and biotic factors on plant performance can shift as succession progresses (Lohbeck et al. 2014, Craven et al.

2018). To our knowledge, our study is the first to build on these findings and demonstrate experimentally that ecophysiological functional traits are the best predictors of TDF tree survival and growth at early- and mid-successional stages (Table 3). Furthermore, we found evidence that the influence of water-use ecophysiological traits on seedling performance decreases during succession in this system, based on our finding that relationships between seedling performance and water-use traits (iWUE, $\Delta \delta^{13}C$, and g_s) were not as strong in the mid-successional interplanted treatment (Figs. 5, 6).

While seedlings had consistently higher growth rates in the cleared treatment (Fig. 4b), these findings may indicate that decreases in air temperature and vapor pressure deficit during the wet season after vegetation is established (Lebrija-Trejos et al. 2011) may lead to decreases in the influence of water-use traits on seedling performance in mid-successional TDF. Ecophysiological functional traits were positively associated with seedling survival and growth in all but one instance (Table 3): in the second year, $\Delta \delta^{13}C$ was negatively associated with cleared treatment growth rates (Fig. 6a). This could indicate integrated WUE (measured with $\delta^{13}C$) for our focal species shifts over time, or that it differs in drought (year 1) versus average precipitation (year 2) years. Because we used values for $\Delta \delta^{13}C$ that were calculated in the first year after planting seedlings in a previous experiment (Werden et al. 2018b), determining how this dynamic trait varies over the lifetime of a seedling is necessary to fully interpret this result. Additionally, to our knowledge no studies have investigated how resource-use strategies shift with ontogeny for all TDF tree life stages. Overlapping traits have now been collected for seedlings, saplings (Derroire et al. 2018), and adults of many TDF tree species (Powers and Tiffin 2010) and future efforts should be dedicated to determining how these trait syndromes shift as TDF communities assemble. In addition to furthering the understanding of how species traits interact with shifting environmental conditions during TDF succession, our results can be used to improve TDF restoration strategies.

Implications for management and design of TDF restoration projects

Recent functional trait-driven approaches have demonstrated how resource-use strategies dictate species performance in active restorations of both tropical wet (Martínez-Garza et al. 2013, Ostertag et al. 2015, Giannini et al. 2017, Charles et al. 2018) and dry forest (Werden et al. 2018b). These studies and others have shown the utility of using functional traits as tools for restoration species selection (Charles 2018) and when designing restorations that have targeted functional outcomes (Laughlin 2014). For these approaches to be effective, it is important to determine which traits are associated with plant performance, which can be highly ecosystem-specific. For TDF in particular, our results demonstrate

that considering ecophysiological traits when designing and implementing TDF restorations greatly improves the prediction of project outcomes. Specifically, we found that TDF restoration effectiveness can be improved by explicitly examining traits related to species-level responses to water limitation, but that binary resource-use strategy categories and leaf and stem traits did not help to improve TDF restoration approaches (Table 3). Moreover, our results highlight the importance of species selection in determining initial TDF restoration establishment, as species identity was highly predictive of seedling survival but there were no differences in overall survival between the two management treatments (Fig. 4a). Additionally, if carbon accumulation is a major project goal, it is important to consider how decreases in the influence of water-use traits on seedling survival and growth (Figs. 5, 6) and increases in belowground resource competition (Fig. 3a) contributed to lower carbon accumulation in the interplanted treatment (Fig. 4b). To increase the probability of restoration success, these findings demonstrate the importance of considering the existing vegetation, or successional status, at a site when designing species mixes.

Initial site conditions such as the level of disturbance or state of remnant vegetation at a site can have lasting effects on the rates of vegetation recovery in tropical forest restoration (Holl et al. 2018). Our results demonstrate that rates of TDF vegetation recovery can also be predictably influenced by planting species mixes with specific functional characteristics. For example, the differences in the strength of TDF tree performance × water-use efficiency relationships between our management treatments (Figs. 5, 6) highlight the importance of planting tree TDF species with high water-use efficiency in sites with high levels of disturbance (cleared). However, water-use efficiency is not as strong of an indicator of TDF species performance at intermediate disturbance levels (interplanted) and it may be more pertinent to consider the importance of biotic factors such as competition when designing species mixes for sites with existing vegetation (Fig. 3a). This finding is constant with the observation from tropical wet forest that species dominance is increasingly influenced by biotic factors as succession proceeds (Lohbeck et al. 2014). It also emphasizes the importance of creating species mixes that are functionally representative of the tree communities that dominate at distinct successional stages to ensure restoration outplantings can establish and persist.

Last, as we showed previously at this site (Werden et al. 2018b), we highlight that it is particularly difficult to restore TDF on degraded Vertisols given that overall survival was low after two years, ranging from 15.1% to 26.4% in the four resource-use strategy × treatment combinations (Appendix S1: Fig. S5). The strongest drought on record in 2015 likely had a large influence on overall survival; however, most of the focal species (eight total) had surviving individuals after two years. Thus, our results demonstrate it is possible to restore TDF on

Vertisols in this region, even during extreme drought. Moreover, our results underscore that clearing existing vegetation before planting seedlings may help catalyze regeneration of TDF on Vertisols, because removing vegetation in a state of arrested succession increased seedling growth rates and may help to establish additional species not abundant on these soils. That said, we caution against using clearing as a management strategy without careful consideration of its benefits and drawbacks.

<h2 style="text-align:center">CONCLUSIONS</h2>

Our results demonstrate that considering how resource-use functional traits describe patterns of TDF tree species' performance not only furthers the understanding of TDF successional dynamics, but also can improve TDF restoration outcomes. In order to do so, it is necessary to focus on traits predictive of survival and growth in this system, namely water-use efficiency and photosynthetic rates. Moreover, our findings suggest that ecophysiological functional traits, specifically those pertaining to water use, had a stronger impact on species performance at early TDF successional stages. Additional focused effort to determine how both environmental conditions and resource competition shift during TDF successional trajectories is necessary to fully understand TDF community assembly.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2116/full

Data Availability

Seedling survival and growth surveys, plot-level environmental data, and remnant vegetation surveys in the interplanted plots are archived in the Dryad Digital Repository: https://doi.org/10.5061/dryad.jm63xsj6p