RESEARCH ARTICLE

Using soil amendments and plant functional traits to select native tropical dry forest species for the restoration of degraded Vertisols

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Abstract

1. Tropical dry forests (TDFs) are critically endangered, and their restoration is understudied. Large-scale passive restoration efforts in north-west (NW) Costa Rica have catalysed TDF regeneration but are not effective on degraded Vertisols, where active restoration is necessary due to high content of shrink–swell clays that impede regeneration following degradation.

2. We established a large-scale restoration experiment in degraded former pastures in NW Costa Rica to determine (1) the restoration potential of native TDF tree species on Vertisols, (2) if plant functional traits elucidate mechanisms behind interspecific variability in species performance and (3) if affordable and readily available soil amendments increase seedling survivorship and growth. We planted 1,710 seedlings of 32 native species coupled with five amendments aimed at ameliorating root-zone microclimatic conditions: sand, rice hulls, rice hull ash, hydrogel and unamended controls. For each species, we quantified a suite of resource-acquisition and ecophysiological functional traits, and monitored survival and growth seasonally over 2 years.

3. Interspecific survivorship after 2 years ranged widely (0%–92.5%). Functional traits including wood density, photosynthetic parameters and upregulation of integrated water-use efficiency, explained interspecific variation in survivorship and growth at distinct ontogenetic stages. Easily measured leaf traits, however, were not good predictors of restoration potential.

4. Hydrogel and sand amendments increased initial seedling survival, but after 2 years no differences among treatments were found.

5. *Synthesis and applications.* We have shown it is possible, albeit challenging, to restore tropical dry forest (TDF) on degraded Vertisols. Our results support the use of functional trait-based screenings to select tree species for restoration projects as tree species with high survivorship and growth in this stressful environment have overlapping ecophysiological functional traits. Furthermore, practitioners should consider water-use and phytosynthetic traits when designing initial species mixes for TDF restorations.

1 | INTRODUCTION

Tropical landscapes have been extensively degraded and deforested, but large-scale passive and active restoration projects have catalysed secondary forest regeneration over the last few decades (Chazdon, 2014). Tropical dry forests (TDFs) have a strong dry season of at least 3–4 months where little to no rain falls (Murphy & Lugo, 1986), which distinguishes TDFs from tropical wet forests, and offers a unique hurdle to restoration projects. Globally, 97% of TDFs are threatened by anthropogenic processes (Miles et al., 2006), and in Central America it is estimated that only 1.7% of the original extent of TDF exists (Griscom & Ashton, 2011; Miles et al., 2006). Despite the fact that TDFs are critically endangered (Janzen, 2002), the restoration of TDFs has been studied minimally compared to wetter tropical forests (Meli, 2003). Following agricultural abandonment in Central America in the 1990s, large tracts of land became available, and active and passive restoration techniques such as plantation establishment, enrichment planting and fire exclusion have been effective in the reestablishment of TDF (Griscom & Ashton, 2011). In north-west (NW) Costa Rica, the conservation of over 160,000 hectares of land in the Área de Conservación Guanacaste created one of the most effective TDF restoration projects in the world (Janzen, 2002). In the Área de Conservación Guanacaste, passive restoration techniques, including removal of unnatural fires and grazers, have been effective in the widespread restoration of TDFs (Janzen, 2002), but active management interventions are necessary (Holl & Aide, 2011) on degraded soils where succession is arrested.

Highly degraded Vertisols, common in NW Costa Rica, are a barrier to the regeneration of TDF on large tracts of land (Gutiérrez, pers. obs.). Vertisols have shrink–swell cycles resulting from high expansive clay content (Deckers, Spaargaren, & Nachtergaele, 2001). Degraded Vertisols shrink and crack during the dry season, and swell during the rainy season, resulting in flooding (Figure 1). Consequently, restoration of these soils is particularly challenging due in part to high seedling mortality rates (Gutiérrez, pers. obs.). To date most studies have focused on developing best practices to use Vertisols for agriculture (Deckers et al., 2001) and not restoration. Most Vertisols in NW Costa Rica were deforested and used for rice cultivation or cattle grazing (Gutiérrez, pers. obs.), and if livestock density is high compaction resulting from grazing can impede restoration (Nepstad, Uhl, & Serrão, 1991). Accordingly, the use of soil amendments during planting may hold promise, as certain amendments facilitate establishment of native TDF seedlings (Fajardo, Rodríguez, González, & Briceño-Linares, 2013). In Vertisols, amendments that ameliorate microclimatic conditions by improving drainage during seasonal flooding may increase initial survivorship and growth when mixed into the rooting zone of seedlings. Other barriers to TDF restoration include selection of

species for plantings, as performance data for native tree species are generally unavailable (Butterfield, 1995).

Plant functional traits, i.e. morphological, physiological or phenological characteristics linked to plant survival, growth or reproduction (Violle et al., 2007), have been effectively used to select species for tropical wet forest restoration projects (Ostertag, Warman, Cordell, Vitousek, & Lewis, 2015). Furthermore, a restoration experiment in a wet forest in Mexico showed some combinations of resource-acquisition functional traits were correlated with survival and growth rates of pioneer tree species (Martínez-Garza, Bongers, & Poorter, 2013). Therefore, using functional traits to understand mechanisms behind species' performance allows results to be extrapolated to other native species with similar traits (Pywell et al., 2003), and ultimately aids the design of restoration plantings that achieve specific outcomes such as rapid carbon sequestration (Ostertag et al., 2015) or restoration of soil fertility (Carpenter, Nichols, Pratt, & Young, 2004). Moreover, defining and identifying the

FIGURE 1 *Top panel*: Image of site in dry season before clearing showing arrested succession *c.* 28 years since abandonment. *Bottom panel*: Flooding in the 2014 wet season after plantings

trait syndromes of TDF species, which are hypothesized to be either conservative (efficient water use/drought-tolerant) or acquisitive (higher water use/drought-intolerant; Lohbeck et al., 2013), could further help to design plantings that achieve specific management goals.

To develop best practices to restore native tree species on degraded Vertisols, we implemented a large-scale TDF restoration experiment in Estación Experimental Forestal Horizontes in NW Costa Rica. Our objectives were to: (1) test the restoration potential of many native TDF tree species on Vertisols, (2) determine if plant functional traits explain interspecific variability in species performance, and thus can be used effectively to choose tree species for restorations, and (3) test if affordable and readily available soil amendments increase initial survivorship and growth of planted seedlings. Although not the focus of our study, we also gathered data for a cost-benefit analysis of these management practices.

2 | MATERIALS AND METHODS

2.1 | Study site

Our experiment was carried out from 2014 to 2016 at Estación Experimental Forestal Horizontes (10.712N, 85.594W) in the Área de Conservación Guanacaste (ACG) in NW Costa Rica. This region has a mean annual precipitation of 1,730 mm with a 5–6 month dry season (December or January–May; www.investigadoresacg.org). During our experiment, sustained wet-season rains did not begin until August for both 2014 and 2015 (Figure S1), leading to the strongest drought on record in this region (IMN Costa Rica, 2015). The site had been abandoned for ~28 years, following decades of rice production and cattle grazing, and received no management since then (Gutiérrez, pers. obs.). Prior to the experiment, the vegetation was in a state of arrested succession (Figure 1), and the few trees that regenerated, out of 21 species observed growing on these soils in the surrounding area, were dominated by only three species: *Cochlospermum vitifolium* (Bixaceae), *Crescentia alata* (Bignoniaceae) and *Guazuma ulmifolia* (Malvaceae) (L.K. Werden, unpublished). A forest inventory study in the same region found 146 tree species in 84 0.1-ha plots (Becknell & Powers, 2014), corroborating that this is a particularly species-poor site.

2.2 | Seed collection and seedling production

Our goal was to collect native species common in the region (Powers et al., 2009), locally abundant on Vertisols, and/or already proven effective in other local restoration projects. We collected seeds from at least three individuals of 38 species in the ACG and stored them in paper bags. All seed was prepared following Román, De Liones, Sautu, Deago, and Hall (2012) and local knowledge, and underwent a 12-hr soak in water to soften seed coats. In early April 2014, seeds were planted into a 3:1 locally collected Inceptisol soil:sand mixture in 5 × 8 cm black polyethylene bags. Seedlings were grown under 90% polyethylene shade cloth for 5 months. Six species with low germination rates were eliminated at this point (Table S1). Seedlings infested with insects were sprayed with diluted insecticide (0.01% w/w Bayer

Decis®, Bayer S.A., San José, Costa Rica) once each in July and August 2014, otherwise they were not sprayed. Before planting, we removed the shade cloth for 2 weeks to harden seedlings in full sun.

2.3 | Experimental design and planting treatments

In June 2014, we cleared existing vegetation from a 1 ha patch of Vertisols with chainsaws and a tractor. In early September 2014, we planted 1,710 seedlings of 32 species (Table S2) into six randomly applied treatment blocks coupled with four soil amendments (sand, rice hulls, rice hull ash and hydrogel) and two unamended controls (to account for variation in microtopography). Soil amendments were selected based on the criteria that they were inexpensive and readily available locally. We used sand, rice hulls and rice hull ash, all thought to increase drainage during seasonal flooding and hydrogel (Hidrokeeper®, Qemi International, Inc., Kingwood, TX, USA), an acrylamide and potassium acrylate copolymer which holds 350% its dry weight in water and extends the wet season by maintaining soil moisture in the rooting zone for 2 weeks following a period with no precipitation.

2.4 | Seedling planting and maintenance

After the onset of wet-season rains in late August 2014, we pre-dug holes in a 1 × 1 m grid for each treatment block. Seedlings were planted over 3 days in early September 2014 at 1 × 1 density, and 10 seedlings of each species were planted randomly by row into each of the six treatment blocks (Figure S2). Some species had insufficient individuals to include in all treatments, so we included these species in as many treatments as we had multiples of 10, resulting in an unbalanced design (Table S3). We applied amendments in standard quantities to individual seedlings, either around (sand, rice hulls and rice hull ash) or below the rooting zone (1 L of hydrogel pre-mixed with water following manufacturer directions). Amendments applied around the rooting zone were mixed into soil extracted from each hole. Holes were subsequently back-filled with the soil/amendment mixture (3:1 soil to sand; 2:1 soil to rice hulls and rice hull ash). Cost analysis for site preparation and planting appear in Appendix S1. Pasture grasses around seedlings were cleared with machetes to avoid competition and shading, in October and November 2014, and in July 2015.

2.5 | Plant functional traits

We measured resource-acquisition and allocation traits assumed to be correlated with species' growth and survival. Plant trait data were collected twice during the experiment to examine how traits changed with ontogeny and in response to field conditions. First, we destructively harvested a subset of seedlings from the nursery to quantify leaf, total biomass and leaf chemistry traits. Second, ecophysiological and leaf chemistry traits were collected (non-destructively) from seedlings after they acclimatized to environmental conditions for 3 months.

In August 2014, we measured leaf traits on seedlings in the nursery using three leaves of five individual seedlings per species. We measured leaf area (cm^2), leaf wet and dry weight (g) dried at 60°C (>48 hr),

leaf thickness (mm) and petiole length (mm) using standard methods (Pérez-Harguindeguy et al., 2013). These data were used to calculate leaf dry matter content (LDMC; g/g), specific leaf area (SLA; cm²/g) and leaf density (g/cm³). Remaining plant material was dried, and roots, shoots and leaves were weighed. We collated additional trait data from previous studies on adult trees in the same region including: leaf habit and compoundness, wood density (Powers & Tiffin, 2010) and maximum height (J.S. Powers, unpublished).

In November 2014, we measured additional traits for all species that still had leaves in the control plots (N = 27). We measured $\Psi_{diurnal}$ ($\Psi_{mid-day}$ − $\Psi_{pre-dawn}$; MPa), a metric used to group species into drought-tolerator or avoider categories (Martinez-Vilalta, Poyatos, Aguade, Retana, & Mencuccini, 2014), with a pressure chamber (PMS Instrument Co., Albany, OR, USA) on two leaves of two individuals per species. We also measured photosynthetic light curves before 11 a.m., following Guzman and Cordero (2013), with a LCi portable photosynthesis system (ADC Bioscientific Ltd., Hoddesdon, UK) on three individuals per species. Following Küppers and Schulze (1985), for each light curve, we calculated: stomatal sensitivity (SS; % per s), stomatal conductance (g_s; mmol m^{-2} s^{-1}), photosynthetic capacity (A_{max}; µmol CO_2 m^{-2} s^{-1}), quantum yield (Φ; µmol CO_2 µmol γ^{-1}), instantaneous water-use efficiency (WUE; µmol CO_2 mmol H_2O^{-1}), dark respiration rate (R_{dark}; µmol m^{-2} s^{-1}) and light compensation point (LCP; µmol m^{-2} s^{-1}). These parameters were included in analyses as they are associated with how plants acquire carbon (A_{max}, R_{dark}; Poorter, 1999) and cope with water stress (WUE, g_s, SS; Galmes, Medrano, & Flexas, 2007), while some directly underlie photosynthetic strategies (LCP, Φ; Poorter, 1999).

Lastly, field and nursery collected leaves (2 leaves per individual × 2 individuals = 4 leaves/species) were dried and transported to Minnesota, USA where they were ground and analysed to determine carbon and nitrogen concentrations, and their stable isotopes, $\delta^{13}C$ and $\delta^{15}N$. The stable isotope of carbon, $\delta^{13}C$, is often interpreted as an integrated measure of WUE (Farquhar, Ehleringer, & Hubick, 1989). We quantified leaf chemical traits at two time points (in the nursery and 3 months after planting) to determine whether whole-plant processes contributing to the regulation of these bulk leaf chemical traits varied with ontogenetic stage, and if patterns of up- or downregulation of these traits after exposure to field conditions correlated with species' performance. From foliar isotope data, we calculated the change in foliar $\delta^{13}C$ values after 3 months in the field as $\Delta\delta^{13}C$ (‰) = $\delta^{13}C_{field}$ − $\delta^{13}C_{nursery}$, where positive values indicate upregulation of integrated WUE. $\Delta \delta^{15}N$ (‰) was calculated in the same way, and positive values represent upregulation of N-fixation for legume taxa.

2.6 | Seedling survival and growth

Survivorship and growth was monitored for every seedling for two wet and dry seasons. We collected survival data every 1–2 weeks between September 2014 and December 2014 to calculate mortality rates related to transplant shock, and subsequent stresses such as flooding. We measured seedling survival, height and diameter at the base and top (at the apical meristem) monthly from September to December 2014 (end of first wet season). The same survey was conducted in July 2015 (end of first dry season), December 2015 (end of second wet season) and again in July 2016 (end of second dry season).

2.7 | Soil properties

In November 2014, we collected 10-cm deep volumetric soil samples (442 cm³) every 5 m on a transect down each block centre using a steel ring. Soil samples were air-dried and sieved (2 mm), soil particle size distribution (sand, silt and clay percentages) determined using the hydrometer method (Bouyoucos, 1962), and soil pH was measured on a 1:2.5 soil:water solution using a Oakton pH electrode.

2.8 | Statistical analysis

We used seedling survivorship and growth surveys to quantify seedling performance over the course of the experiment. Unfortunately, 265 planted seedlings were accidentally destroyed during the first grass clearing in October 2014. These individuals were omitted from statistical analyses; thus, the total number of seedlings was N = 1445 (Table S3). We defined time periods representing distinct stages that had a specific hypothesized influence on seedling growth and survival (Table 1), and for each time period, we computed survivorship percentages and relative growth rates (RGR). Due to our experimental design, some parameters were calculated at the species-level (survivorship percentages) and some were calculated for individual seedlings (RGR). We calculated RGR for both height (RGR_{ht}; ln(cm) per day) and stem volume (RGR_{vol} calculated as the volume of a conical frustum; ln(cm³) per day) for each seedling using the classic RGR equation: (ln[final height or volume] − ln[initial height or volume])/(final day-initial day) (Hoffmann, 2002). RGR values were calculated for each time period to evaluate changes in RGR over time. We quantified RGR during the dry season because some species we planted are evergreen (Table S2) and may grow year-round. Over the course of our experiment, RGR did not slow or approach an asymptote, thus the assumptions required of the classic RGR model were met (Paine et al., 2012).

Seedling survival and RGR for each time period were the main response variables of interest. We used visual assessments of survivorship among species, and performed type-III ANOVAs (for unbalanced

TABLE 1 Time periods of interest used to compute survivorship and growth metrics, and assumed influence of each on planted seedlings

Time period	Stage	Influence on seedlings
September–October 2014	Transplant shock	Planting influence on seedlings
September–December 2014	First wet season	First exposure to field conditions
January–June 2015	First dry season	First water limitation
July–December 2015	Second wet season	First wet season not impacted by planting
January–June 2016	Second dry season	Second water limitation

data) using RGR as the response during different time periods, to quantify species performance (Objective 1). We calculated Pearson correlations, with Bonferroni corrections for multiple comparisons ($N = 5$ time periods), and used linear regression, to investigate relationships between functional traits and species-level survivorship and RGR (Objective 2). When conducting analysis of soil amendment effectiveness (Objective 3), we considered how results differed for species that are 'viable' for future Vertisol restoration projects, which we defined as species with ≥10% survivorship at the conclusion of the experiment. We used logistic regression to predict the probability of seedling survival in different amendment treatments; these analyses were run twice, once including all species and once for restoration-viable species. The performance of planted seedlings in soil amendments was quantified in terms of RGR with type-III ANOVAs, with soil amendment and restoration viability as predictors. Pairwise comparisons between seedling survival and RGR in each soil amendment were made using Tukey's HSD. To test for differences in soil properties between the six planting blocks we performed Tukey's HSD post hoc tests on one-way ANOVAs with each soil variable (pH, % sand, silt and clay) as responses, and treatment block as the predictor. All analyses were conducted in R 3.2.3 (R Development Core Team, 2016).

3 | RESULTS

3.1 | Soil properties

Soil clay concentrations ranged from 41.6% to 71.2% and pH values from 5.48 to 6.09. Nonetheless, we found no significant pairwise differences (Tukey's HSD; $p < .05$) in soil particle size distribution or pH among the six treatment blocks (Appendix S2).

3.2 | Overall species survivorship

Over all treatments, survivorship to 2 years had a large range, from 0% to 92.5% among species (Figure 2, Table S2). Of the 32 species, 20 had survivorship of <10% and 15 of those 20 species had no surviving individuals. The remaining 12 species were considered restoration-viable, all of which had survival rates ≥10.9%, and 7 of which had >30% survival overall.

3.3 | Functional traits and seedling survival

Values for most functional traits had large interspecific ranges, with coefficients of variation for individual traits ranging from 3.02% for foliar $\delta^{13}C_{nursery}$ to 208.63% for seed mass (Table S4). The only trait correlated with survival when the experiment concluded was $\Delta \delta^{13}C$ ($r = .53$, $p < .01$, Table 2), indicating that the trait most predictive of long-term seedling survival was the ability to upregulate integrated WUE ($\Delta\delta^{13}C$). Distinct trait groups were correlated with survivorship at different ontogenetic stages (Table 2), but no relationships were found between survival and life-history traits (leaf habit, leaf compoundness or seed dispersal syndrome) (Tukey's HSD; data not shown). During transplant shock and the first wet season, wood
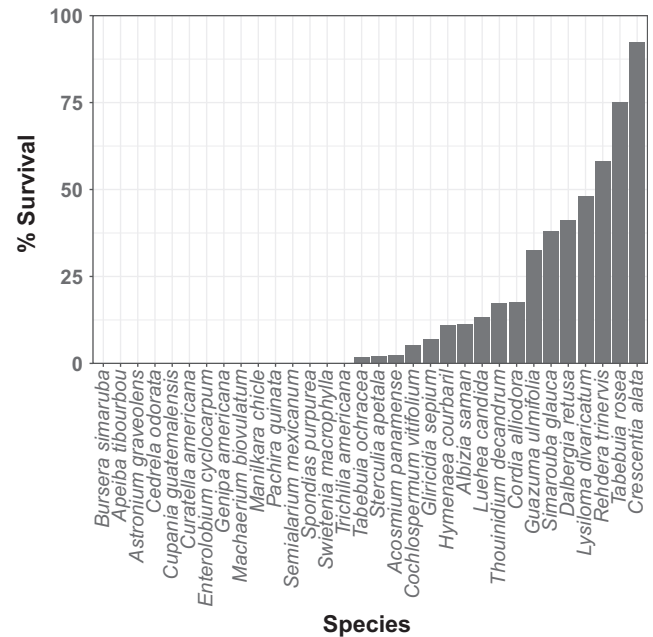

FIGURE 2 Overall species survival percentages after 2 years for tree seedlings planted on degraded Vertisols in a tropical dry forest

density and leaf chemistry traits (C and N %) were correlated with species survival, but following the first water limitation (first dry season), all trait–survivorship relationships were driven by photosynthetic (g_s, A_{max}, R_{dark}, LCP) and/or water-use traits (g_s, WUE, $\Delta\delta^{13}C$).

Wood density was the best predictor of survivorship during both transplant shock ($r = .58$, $p < .001$), and the first wet season ($r = .55$, $p < .001$), as species with higher adult wood densities had higher rates of early survival. For field-collected leaves, foliar C % was positively correlated ($r = .50$, $p < .01$), and foliar N % negatively correlated ($r = -.50$, $p < .01$) with survival during the first wet season. After the first wet season, photosynthetic and water-use traits were the only traits predictive of survival. During the first dry season, high photosynthetic trait values (g_s: $r = .43$; A_{max}: $r = .50$; R_{dark}: $r = -.60$; LCP: $r = .40$; $p < .01$ for all), instantaneous WUE (WUE: $r = .50$, $p < .01$), and upregulation of integrated WUE ($\Delta\delta^{13}C$: $r = .50$, $p < .01$; Figure 5) increased survival. These relationships held through the second wet season except for LCP and g_s.

3.4 | Functional traits and RGR

A similar set of photosynthetic and water-use traits were correlated with seedling RGR, and these relationships differed slightly by time period when RGR was expressed for height (RGR_{ht}; Table S5) or volume (RGR_{vol}; Table S6). RGR_{ht} and RGR_{vol} were highly correlated ($p < .001$) during transplant shock, the first dry season, and second wet season, but not for the first wet season and second dry season (Table S7). We therefore address relationships between RGR_{ht} and RGR_{vol} and traits separately for the first wet season and second dry season.

During transplant shock, shoot dry mass was predictive of RGR_{ht} ($r = -.47$, $p < .01$), and R_{dark} predictive of RGR_{vol} ($r = -.65$, $p < .001$).

TABLE 2 Pearson correlations for species-level traits and survivorship percentages at specific time periods (see Table 1)

Functional trait	Time period				
	Transplant shock	First wet season	First dry season	Second wet season	Second dry season
Leaf, stem and biomass					
Seed mass (g)	0.19	0.15	−0.12	−0.12	−0.12
Leaf area (cm^2)	0.01	−0.14	−0.2	−0.23	−0.26
Petiole length (mm)	−0.15	−0.23	−0.19	−0.25	−0.31
Leaf thickness (mm)	−0.05	−0.02	0.01	−0.02	−0.01
LDMC (g/g)	0.37*	0.40*	0.01	0.06	0.12
Leaf density (g/cm^3)	0.26	0.27	0.12	0.17	0.21
SLA (cm^2/g)	0.29	0.20	−0.22	−0.19	−0.16
Wood density (g/cm^3)	**0.58****	**0.55****	0.04	0.08	0.13
Shoot dry mass (g)	0.14	0.03	−0.07	−0.07	−0.07
Root dry mass (g)	0.10	0.09	0.17	0.18	0.17
Root/shoot ratio (g/g)	−0.20	−0.16	−0.14	−0.11	−0.09
Maximum adult height (m)	0.07	0.02	−0.09	−0.11	−0.12
Ecophysiological					
SS (% per s)	0.26	0.22	0.04	0.07	0.09
g_s (mmol m^{-2} s^{-1})	0.09	0.06	**0.43***	0.40*	0.37*
A_{max} (µmol CO_2 m^{-2} s^{-1})	−0.19	−0.15	**0.50***	**0.48***	0.45*
Φ (µmol CO_2 µmol $γ^{-1}$)	−0.26	−0.31	0.26	0.26	0.26
WUE (µmol CO_2 mmol H_2O^{-1})	−0.26	−0.23	**0.50***	**0.48***	0.44*
R_{dark} (µmol m^{-2} s^{-1})	−0.39	−0.48*	**−0.60***	**−0.56***	−0.54*
LCP (µmol m^{-2} s^{-1})	0.43	0.52*	0.40*	0.35	0.34
$Ψ_{diurnal}$ (MPa)	−0.37*	−0.36*	−0.23	−0.28	−0.30
Leaf chemistry					
Foliar C % (field)	0.43*	**0.50***	0.07	0.06	0.09
Foliar C % (nursery)	0.32	0.35*	−0.08	−0.08	−0.05
Foliar N % (field)	−0.42*	**−0.50***	−0.08	−0.13	−0.17
Foliar N % (nursery)	−0.22	−0.31	−0.34	−0.34	−0.34
$δ^{13}C_{field}$ (‰)	−0.23	−0.01	0.29	0.24	0.22
$δ^{13}C_{nursery}$ (‰)	−0.39	−0.36	−0.31	−0.39	−0.43*
$δ^{15}N_{field}$ (‰)	0.19	0.36	0.24	0.25	0.25
$δ^{15}N_{nursery}$ (‰)	−0.16	−0.14	0.03	0.01	−0.01
$Δδ^{13}C$ (‰)	0.09	0.26	**0.50***	**0.52***	**0.53***
$Δδ^{15}N$ (‰)	−0.28	−0.37	−0.12	−0.14	−0.16

Pearson correlation coefficients are shown with two-tailed Bonferroni corrected significance (α = 0.05/5 tests: cut-off $p < .01$) indicated with bold text. Significant uncorrected two-tailed p-values are indicated by *$p < .05$; **$p < .01$; ***$p < .001$.
LDMC, leaf dry matter content; SLA, specific leaf area; SS, stomatal sensitivity; WUE, water-use efficiency; LCP, light compensation point.

Like survivorship and trait correlations (Table 2), photosynthetic and water-use traits only predicted RGR_{ht} for the second wet season. The magnitude of correlations between these traits and RGR_{ht} during the second wet season was the highest for any trait and time period: g_s: $r = .60$; A_{max}: $r = .82$; Φ: $r = .68$; WUE: $r = .80$ ($p < .001$ for all). Notably, photosynthetic (R_{dark}: $r = −.70$, $p < .001$; g_s: $r = .46$, $p < .01$) and instantaneous WUE ($r = .47$, $p < .01$) traits predicted RGR_{vol} during the first wet season, the only instance these traits

predicted growth or survival before the first dry season. During the first dry season, the only trait correlated with RGR_{ht} was petiole length ($r = −.56$, $p < .01$) and no traits were predictive of RGR_{ht} or RGR_{vol} during the second wet season. Also notable, although not significant with Bonferroni correction, maximum adult height was negatively correlated with RGR_{ht} for every time period except the second wet season ($p < .05$; Table S5), indicating that trees of short stature as adults had higher overall RGR_{ht}.
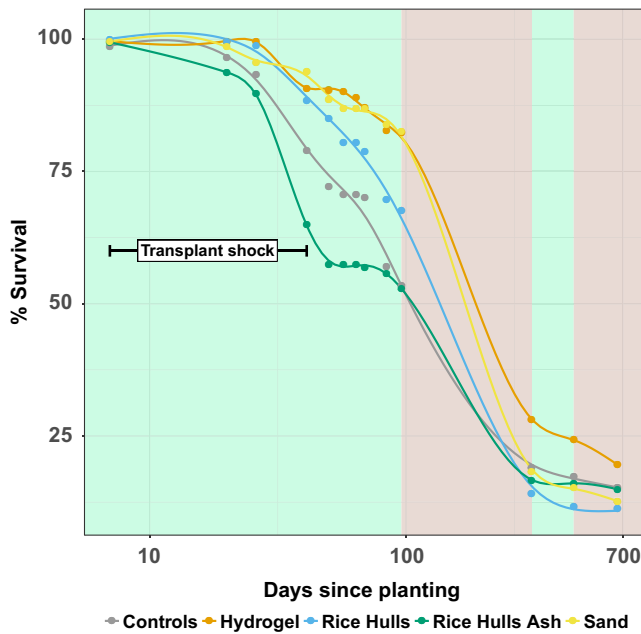
FIGURE 3 Overall percent seedling survivorship grouped by soil amendment. Green shaded regions are the wet seasons, and tan shaded regions are the dry seasons. The x-axis is on a logarithmic scale to highlight mortality occurrence during early surveys. Trend lines displayed were fit using a generalized additive model with a penalized smoother

3.5 | Relationships between "soft" and "hard" functional traits

LDMC was the only "soft" (easily measured), trait correlated with any "hard" traits (requiring specialized equipment to quantify). LDMC was significantly correlated with A_{max} ($r = -.6$, $p < .001$), and instantaneous WUE ($r = .54$, $p < .01$; data not shown). No "soft" traits were correlated with $\Delta \delta^{13}C$.

3.6 | Soil amendments and survivorship

There were large differences in seedling survivorship among soil amendment treatments during the first wet season, but survivorship converged following the first dry season (Figure 3). The rank order of survivorship after the first wet season was: hydrogel = sand > rice hulls > rice hull ash = controls (Tukey's HSD; Figure 4a), and this pattern was essentially the same for restoration-viable species survivorship (Figure 4b). While by rank seedlings planted with hydrogel consistently had the highest survivorship (Figure 4), survivorship did not differ statistically among soil amendments after 2 years (Figure 4e,f).

3.7 | Soil amendments and relative growth rates

Soil amendments did not alter mean RGR_{ht} for any period except the final dry season ($F = 3.03$; $p = .019$; Table S8). During this period,

seedlings planted with hydrogel had <1% lower RGR_{ht} ($p = .003$; Tukey's HSD) than control seedlings. RGR_{vol} was influenced by soil amendments for several time periods. During transplant shock, the rank order of increases in mean RGR_{vol} relative to the controls was: sand = rice hull ash > controls (sand: 32% higher, $p < .001$; rice hull ash: 25% higher, $p = .018$; Tukey's HSD). Finally, during the first wet season, RGR_{vol} in the rice hull ash treatment was 33% higher than the controls ($p < .001$; Tukey's HSD).

4 | DISCUSSION

We have shown it is possible, albeit challenging, to establish native TDF species on degraded Vertisols. In our species screening trial, overall seedling survivorship at 2 years was very low, and only three species attained survival rates >50%. These results suggest that continued active management will be essential when restoring TDF on Vertisols. Species with high performance in this stressful environment had some overlapping functional traits, namely the ability to upregulate integrated WUE after planting and to maintain high rates of photosynthesis and instantaneous WUE. Explicitly considering water-use and photosynthetic traits when selecting species for plantings could greatly increase initial effectiveness of TDF restoration projects on degraded soils. While certain soil amendments increased short-term survivorship, no amendment influenced survivorship after 2 years.

4.1 | Viable species for Vertisol restoration

NW Costa Rica experienced two of the most extreme drought years on record during our experiment, and droughts such as these are becoming more common (IMN Costa Rica, 2015). A natural drought event was therefore imposed on our experiment, and species with the highest survival rates (Figure 2) are not only suitable for Vertisols plantings, but are also likely to tolerate future rainfall deficits. For comparison, an experiment in the same conservation area found some of the species we used (*Hymenaea courbaril* and *Swietenia macrophylla)* had 50% higher survival when planted in non-drought conditions on less-degraded soils (Gerhardt, 1993). Much lower survivorship should therefore be expected in Vertisol restorations and/or during drought, but could be partially remedied with management strategies such as replanting seedlings in subsequent years or initially planting multiple seedlings at each hole, and subsequently thinning. Despite these challenges, we identified a diverse group of species tolerant of these harsh conditions.

The species we found to be restoration-viable exhibit diverse life-history traits, and could be used to design planting mixes (Table S2). In terms of leaf habit and dispersal syndrome, almost all restoration-viable species were deciduous and wind dispersed, apart from two animal dispersed species not common on Vertisols (*Hymenaea courbaril* and *Simarouba glauca*), and one evergreen species (*Simarouba glauca*). Three nitrogen-fixing legumes (*Lysiloma divaricatum*, *Dalbergia retusa* and *Albizia saman),* which have restored
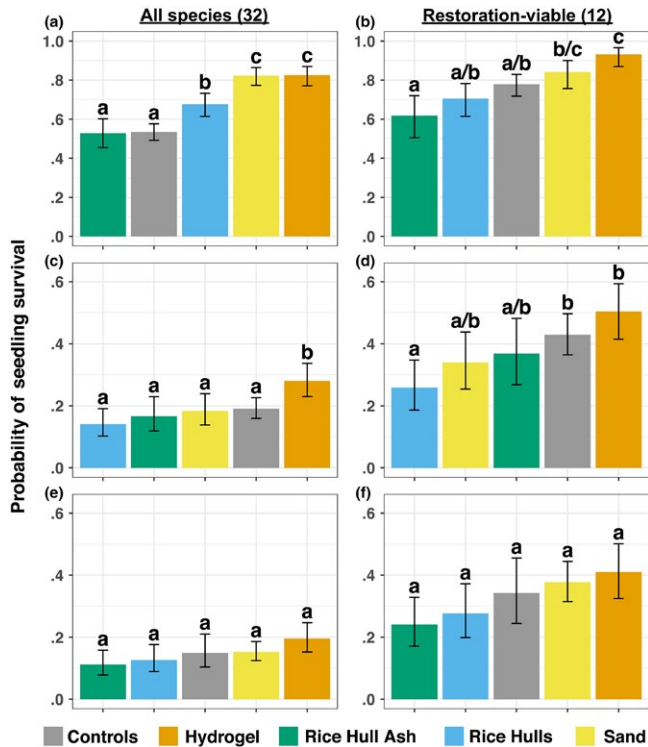
FIGURE 4 Seedling survival percentages predicted by logistic regression for each treatment. Survival probabilities are shown for all species in the left column (N = 32), and restoration-viable species in the right column (N = 12). Panels (a and b) are the first wet season, (c and d) the first dry season, and (e and f) survival after 2 years. Error bars are 95% confidence intervals, and letters indicate significant (p < .05) differences among groups (Tukey's HSD)

soil fertility in other Costa Rican restorations (Carpenter et al., 2004; Gei & Powers, 2013), provide further utility for Vertisol restoration projects. Not surprisingly, species with the highest (*Crescentia alata*; 92.5%) and seventh highest (*Guazuma ulmifolia*; 32.6%) survival rates are two of the most common tree species on Vertisols at this site, but most other species we found to be restoration-viable are rarely found on Vertisols, or at all (L.K. Werden, unpublished), and seed dispersal limitation could be a barrier to their re-establishment (Janzen, 2002).

4.2 | Functional traits and seedling survival and growth

Water limitation during early TDF succession may influence species composition by favouring drought-tolerant species with conservative trait syndromes (Lohbeck et al., 2013). Consistent with this framework, the only trait we found to predict survivorship through the conclusion of our experiment was the ability to upregulate integrated WUE ($\Delta\delta^{13}C$; Table 2). From the traits, we measured, $\Delta\delta^{13}C$ may be the most important to consider when the management goal is to select drought-tolerant species for TDF restorations. None of the so called "soft" leaf traits we quantified predicted survivorship, and only one leaf trait was predictive of RGR (petiole length), and only

during the first dry season (Table S5). This is consistent with findings from a Mexican wet forest, where leaf traits only predicted survivorship and growth of a limited group of pioneer tree species (Martínez-Garza et al., 2013). Notably, LDMC, a "soft" trait, was correlated with both A_{max} and instantaneous WUE, and LDMC could be an acceptable proxy for traits requiring specialized equipment to measure. $\Delta\delta^{13}C$, was not correlated with any "soft" leaf traits, but is inexpensive to quantify.

At other ontogenetic stages, but not through the conclusion of the experiment, species with conservative trait values (high instantaneous WUE; Lohbeck et al., 2013; high wood density; Lohbeck et al., 2013; high C and low N%; Ostertag et al., 2015) were most likely to survive (Table 2). However, we also found species with high survivorship had photosynthetic traits on the acquisitive end of the spectrum (high A_{max} and g_s, low R_{dark}; Bazzaz & Pickett, 1980; Table 2), which precludes simple categorization of restoration-viable species as having conservative or acquisitive strategies.

Conservative values of both instantaneous WUE and $\Delta\delta^{13}C$ were positively correlated with species' survivorship and growth after exposure to high irradiance and temperatures during the first dry season (Tables 2, S5 and S6). Species with high adult wood densities (conservative values) were more likely to survive during transplant shock and the first wet season, but not during any other period (Table 2). In this region, community weighted mean wood densities were typically highest during early succession (Becknell & Powers, 2014), perhaps because legumes, abundant in young regenerating forests (M.G. Gei, pers. comm.), have high wood densities (Powers & Tiffin, 2010). Notably, we found four species with the highest survivorship were legumes. The last group of traits with conservative values, while only predictive of survival during the first wet season, showed species with high foliar C and low N % had higher overall survival (Table 2). By contrast, high-performing species had acquisitive strategies for some photosynthetic parameters.

After the first dry season, species with acquisitive values (high) of A_{max} and g_s in the field were more likely to survive. This could be attributed to the fact that these species are better adapted to drought conditions in Vertisols as they were simultaneously able to maintain high levels of photosynthesis and integrated WUE (Table 2, Figure 5). The same photosynthetic parameters (A_{max}, g_s and WUE) were also positively correlated with RGR_{ht} during the second wet season (Table S5), consistent with the idea that species best adapted to Vertisols were those with the highest RGR during the first full wet season after planting. Trees with higher maximum adult heights appear to have lower RGR_{ht} in every period except for the second wet season (p < .05, NS with Bonferroni correction; Table S5), consistent with our observation that short stature trees are dominant at our site (Werden, pers. obs.). Lastly, R_{dark} was negatively correlated with survival from the first dry season forward, and with RGR_{vol} during the first wet season, and we are not aware of a mechanism that explains this result.

4.3 | Soil amendments and survival and growth

No soil amendment significantly increased overall survivorship to 2 years (Figure 4e), although the exceptional drought during our
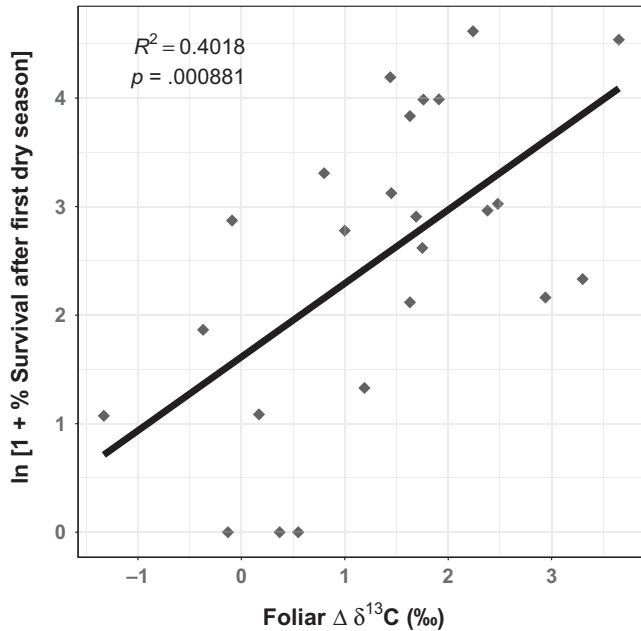
FIGURE 5 Species survival percentages after the first dry season plotted against foliar $\Delta\delta^{13}C$ calculated using leaves collected from seedlings before and after planted

experiment may have decreased amendment effectiveness. A caveat to our study is that, for logistic reasons, we did not have sufficient seedlings to plant replicate treatments in multiple blocks. Additionally, while there were significant differences in clay and sand percentages among blocks, Tukey's HSD tests suggest pairwise differences in soil properties among blocks were slight, as only three marginally significant differences were found when comparing between blocks (Appendix S2). Therefore, these uncontrolled variables may have affected our results, but they do not invalidate our main conclusion that no differences among amendments were found after 2 years. We did find seedlings planted with hydrogel always had the highest survival by rank (Figures 3 and 4), consistent with an experiment that found hydrogel to increase seedling survivorship in TDF (Fajardo et al., 2013). Both sand and hydrogel increased survivorship over the controls through the first wet season (Figure 3). We therefore recommend testing the effectiveness of applying sand and hydrogel simultaneously, as the two amendments serve different functions. Hydrogel also improved survivorship through the first dry season, and could be providing water to seedlings after dry season onset (Figure 4c). While sand and rice hulls increased RGR over the controls during transplant shock, and rice hull ash increased RGR during the first wet season, no soil amendment predictably influenced seedling growth (Table S8). Lastly, we estimate costs to apply the tested amendments are minimal, from ~$3 to $100 per hectare at standard planting densities (Appendix S1).

5 | CONCLUSIONS

Our results suggest functional trait-based screenings of tree species for restoration projects may help restoration practitioners efficiently select species for restoration projects. Furthermore, consistent with other studies, we found leaf traits are weak predictors of species' survival and growth, and the traits most predictive of survivorship and growth in TDF correspond to how species capture carbon and tolerate drought. In particular, species that upregulated integrated water-use efficiency ($\Delta\delta^{13}C$) had the highest long-term survivorship and restoration potential. Lastly, our experiment helped to determine which native tree species and functional traits are important to consider when re-establishing TDF on degraded Vertisols.

AUTHORS' CONTRIBUTIONS

L.K.W., M.G.L. and J.S.P. designed the experiment. L.K.W., P.A.J., S.Z., E.C.M. and E.M.S. implemented the experiment and collected data. L.K.W. performed statistical analyses. L.K.W. and J.S.P. interpreted results and wrote the manuscript, and all others contributed to revisions.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.fd57r (Werden et al., 2017).

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