

UN DECADE ON ECOSYSTEM RESTORATION

RESEARCH ARTICLE

Winners and losers in dryland reforestation: species survival, growth, and recruitment along a 33-year planting chronosequence

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Reforestation in the Lower Rio Grande Valley (LRGV) of Texas began in the 1960s and to date over 6,475 ha of land has been reforested. However, there has been minimal assessment to understand differential species success, compositional trends, and the aboveground carbon sequestration potential of these developing forests. We coupled quantitative planting information of >50 native woody tree and shrub species with surveys of 5,223 stems of 4,606 individuals in a chronosequence of restored forests ranging in age from 1 to 33 years to estimate species-specific mortality rates, biomass accumulation and recruitment, as well as compositional trends in the herbaceous understory. We show that 7–15 years are required for mortality rates of the transplanted cohort to stabilize to background levels observed in other dry forests. A small number of species, mostly N-fixing trees with a deep rooting habit, persisted on the landscape beyond 15 years. Even so, aboveground biomass (corrected for differences in initial planting density) accumulated at an average rate of 1.41 Mg ha⁻¹ yr⁻¹ compared to 0.35 Mg ha⁻¹ yr⁻¹ for a fallow old-field. Species biomass growth rates increased with decreasing mortality, as did the abundance of recruits, suggesting a degree of reproduction by initial planted cohorts. However, a suite of highly competitive exotic grasses increases in density over a 25-year period, which we link to suppressed seedling recruitment. This poses a serious challenge to the long-term sustainability of planted forests in the LRGV. We highlight potential avenues of research and modification to restoration methodologies.

Key words: carbon sequestration, drylands, forest demography, invasive grasses, seedling survival, semiarid, Tamaulipan thornscrub

Implications for Practice

- Combining forest chronosequences with detailed planting information is a useful tool for evaluating restoration effectiveness on a species-specific basis.
- Planting a species-diverse cohort of tree seedlings as a one-and-done strategy to restore biodiversity in abandoned agricultural lands does nothing to prevent the establishment and spread of invasive grasses. These grasses limit recruitment in more developed stands and their management is critical for long-term success.
- Many species are ill-suited for open fields of dryland regions. Research is needed to evaluate costs and benefits of two approaches to this problem: greater up-front investment in seedling establishment through shelters and additional moisture, or staggered multiphase planting into cohorts of early, mid, and late successional species.

Introduction

Semiarid areas are being increasingly targeted for forest restorations to address severe degradation, biological invasion, and associated loss of resource provisioning for society and wildlife (Marshall et al. 2012; Song et al. 2018). Although

the potential for carbon sequestration in dryland forests is lower than that of many other biomes, these forests play an important role in the global carbon cycle by virtue of their sheer extent globally (Bastin et al. 2017; Erb et al. 2018; Rotenberg & Yakir 2010). For these reasons, assessments of restoration projects in these ecosystems are urgently needed to inform future efforts.

The Lower Rio Grande Valley (LRGV) of south Texas is host to a biologically diverse assemblage of communities (Jahrsdoerfer & Leslie 1988; Leslie 2016). Although plant species richness

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at small spatial scales (km^2) is comparable with that of the broader southern United States, unusually sharp gradients in both precipitation and hydro-edaphic conditions across the region cause rapid species turnover, which results in high beta diversity in both flora and fauna (Flores 2019; Perez et al. 2021). Numbers of bird and Lepidopteran species regionally are among the highest in the continental United States, and many species of plants and animals found in the region have very limited distributions within the United States and are more widespread in Mexico and Central America (Stanford 1993; Brush 2015; Jenkins et al. 2015; Kartesz 2015; Saghatelian 2017). The historic areal extent of undisturbed habitat in the LRGV is believed to have been reduced by over 95%, with a slightly higher rate in the Rio Grande floodplain than in areas more distant from the river (Leslie 2016).

The need for habitat restoration and increased intra-patch connectivity is clear, and consequently, the LRGV is being increasingly targeted for reforestation in both carbon-based and endangered species habitat initiatives. Beginning sporadically in the 1950s and annually in 1982, the Texas Parks and Wildlife Department and U.S. Fish and Wildlife Service (FWS) began to reforest plots of retired agricultural land in the LRGV to increase forested area and inter-patch connectivity (Vora 1992; Judd et al. 2002; Ewing & Best 2004). Between 1982 and 2020, an average of approximately 170 ha were reforested per year by FWS, totaling at least 6,475 ha as of this publication, and over 5 million seedlings have been planted during that time (K. Wahl, unpublished data). Ongoing thornscrub restoration is geared toward enhancing both native plant biodiversity as well as the provision of habitat for all thornscrub-obligate species, including migratory birds.

Despite the scale and expense of this project, post-planting assessments of seedling survival, species recruitment, and forest development are lacking and the few studies which have been carried out have focused solely on seedling growth and survival and for a maximum of 2 years post-planting (Alexander et al. 2016; Dick et al. 2016; Mohsin et al. 2021). Chronic drought and extreme summer heat pose significant challenges to seedling survival in the LRGV, especially in the context of old-field restoration where established woody nurse plants are absent and soil structure and organic content may be impaired. Annual mortality rates of seedlings within their first 1 to 2 years post-planting growth can be high in this context, even when outplanted after germination and early development in a production nursery. Overall mortality in a study of 3,600 seedlings carried out at Sal del Rey between November 2018 and October 2019 was observed to be 21%, although rates varied from 8 to 69% by species, and mortality of seedlings subject to similar conditions at the Laguna Atascosa National Wildlife Refuge were approximately 15% after 2 years (Alexander et al. 2016; Dick et al. 2016; Mohsin et al. 2021).

Although not an immediate threat to the survival of planted individuals within the first few years of growth, a long-term challenge to successful reforestation is the possibility that woody species' eventual reproduction may be depressed by biological invasion of the herbaceous layer to a rate below that

necessary for maintenance of the species on the landscape (Flory & Clay 2010; Dick et al. 2016). Widespread invasion of the understory of restored forests by several species of aggressive, non-native grasses is suspected to have reduced recruitment of native woody species (Marshall et al. 2012). Strong depression of biodiversity by *Cenchrus ciliaris* L. (buffel-grass, one of the three most important invasive grasses in south Texas) has been observed in Australia, where it is also invasive (Clarke et al. 2005). If that relationship can be extended to the LRGV, then invaded forests of south Texas may degrade into a non-native savannah as mature trees begin to die without a sufficient density of replacement in the subcanopy. In sum, decadal trends in growth, survival, and recruitment remain key unknowns within the context of LRGV reforestation.

The staggered nature of reforested plots' development times, as well as shared land use history, in this region creates a situation conducive to the use of a chronosequence (Foster & Tilman 2000). Chronosequence studies are a powerful tool for estimating vegetation dynamics over decadal to millennial time scales, by substituting space for time at sites which are near-identical in terms of initial state and environmental conditions and differ only in the duration for which they have been developing (Walker et al. 2010). Chronosequences have been successfully used to chart changes in vegetation characteristics and ecosystem functioning at a variety of temporal scales (Lichter 1998; Lebrija-Trejos et al. 2010). To our knowledge, no study has yet combined the chronosequence approach with detailed initial planting data to quantify species-specific vital rates over decadal timescales within a restoration context (Ewing & Best 2004). Such an approach is poised to yield important insights into early successional dynamics and can be used to improve restoration practices.

In this paper, we use a combined chronosequence-planting approach to address several questions associated with vegetation dynamics and the developmental trajectory of reforested communities. This series of surveys was undertaken to quantify the relative survival, growth, and recruitment rates of mostly woody species planted in an initial reforestation effort at multiple durations post-planting, as well as the change with time of forest structure, aboveground biomass of woody plants, and areal coverage in native versus non-native herbaceous species. Results of these surveys will inform future restoration efforts in this region. Additionally, in a region relatively understudied in terms of the makeup of its vegetation communities (Flores 2019), this study provides critical baseline estimates of species performance within an early successional context. Species performance, when paired with plant functional traits, may be useful for understanding long-term dynamics of both restored and undisturbed communities (McGill et al. 2006). Our questions are related to four important unknowns:

- (1) *Community-level status and trends of woody plant abundance, biomass, and mortality.* Is woody plant abundance and biomass saturating at 30 years or are further increases likely? What are the contributions of planted versus naturally recruiting individuals to observed trends? How long does it take for mortality of the planted cohort to stabilize?

- (2) *Interspecific patterns and drivers of survival, growth, and recruitment.* Do growth, mortality, and recruitment rates covary at the species level? Which plant functional traits are associated with differential species success?
- (3) *Trends in species composition and relative importance of planting versus recruitment.* As plots age, are communities shifting toward dominance by a small number of species? Does natural regeneration yet comprise a significant fraction of aerial biomass for any species, and what are the near-term (next 5–7 years) trends in planted versus recruited biomass?
- (4) *Trends in herbaceous community composition and controls over seedling recruitment.* How does the herbaceous community change with time and how does it, as well as woody canopy cover, impact seedling recruitment?

Methods

Study Sites

In total, this study encompasses seven plots across two sites, the Sal del Rey and Teniente tracts of the LRGV National Wildlife Refuge (hereafter “the Refuge”). Plots span in age (time since planting or direct seeding) from 1 to 33 years: one 1-year census of a recently published intensive study at Sal del Rey (Mohsin et al. 2021; only control seedlings with no shelters), four additional plots at Sal del Rey, and two at Teniente (Fig. 1). The need to sample individual plots extensively to estimate species survival from planting information (see below) precluded us from distributing our sampling effort as smaller sampling units across replicate plots of similar ages, as is recommended for chronosequence studies (Walker et al. 2010). However, we have reason to believe these plots are following similar trajectories, as they

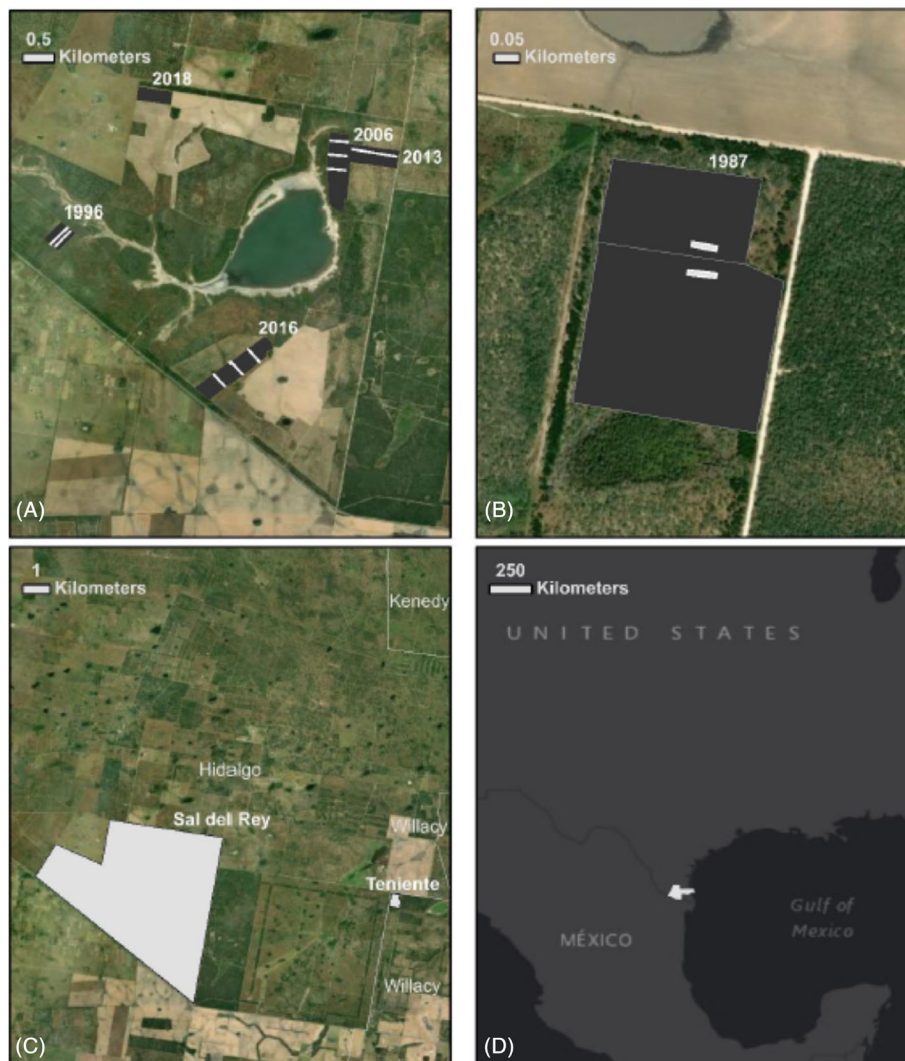


Figure 1. Maps of study sites. (A) Location of plots and transects on the Sal del Rey tract. Dark gray polygons represent reforestation plots and light gray polygons survey transects. (B) Location of plots and transects on the Teniente tract. (C) Location of tracts relative to each other. (D) Location of site relative to the United States, Mexico, and Gulf of Mexico.

share similar soil types and have a similar shared land use history and common method of reforestation encompassing a shared complement of planted species (Soil Survey Staff 2021; Table 1 & S1). Notably, all sites included in this study are underlain principally by fine sandy loams and sandy loams, with only minor inclusion of sandy clay loams at two sites (Table 1). Soils are entirely devoid of rocks and no water-restrictive layer was present within the upper 2 m. Nonetheless, repeat surveys and surveys of replicate plots of similar ages will offer insight into year-to-year variability in species survival patterns and will be the subject of future work. For a full description of physiographic context, reforestation history and methods, see Supplement S1 and Figure S1.

Field Assessments

We sampled for mature individuals separately from seedlings and saplings. Surveys of mature individuals, defined here as those with a stem diameter at ground height (DGH) greater than 5 cm, were conducted using 10-m wide transects of varying lengths, but always oriented perpendicular to planting rows (Table S2; Fig. S2); the total area of which is denoted by A_{mature} (m^2). A_{mature} totaled approximately 0.67 ha for most plots, which represented 2–7% of total planted plot area (Table 1). Coordinates and species identity of all mature individuals rooted partially or wholly within the transect area were recorded and measured for DGH (cm) and height perpendicular to ground (m). For seedlings and saplings, defined here as individuals with a DGH less than 5 cm, we used four 1 m^2 quadrats per 10 m of transect linear distance to sample (Fig. S2), and the total sample area for seedlings and saplings, $A_{seedling+sapling}$ (m^2), totaled 185–313 m^2 across plots. 1 m^2 quadrats were not sampled at the 1-year site at Sal del Rey because all individuals present were seedlings and were measured individually. No seedling data were recorded at Teniente. Species identity, DGH, and height of each stem ≤ 5 cm DGH were recorded. In all surveys, each stem of multistemmed individuals, which comprised 31% of all mature individuals (245 out of 782; $>90\%$ of which come from the family Fabaceae), were measured separately. Number density in any plot p for any given species i ($N_{p,i}$; ha^{-1}) was estimated by dividing the number of individuals found by the sample area for mature and seedling/saplings separately, followed by summation ($N_{p,i} = N_{mature,p,i}/A_{mature,p} + N_{seedling+sapling,p,i}/A_{seedling+sapling,p}$).

Within seedling and sapling quadrats, percent coverage of groundcover classes and woody species canopy were visually assessed, the recorded value of any given class being the mean of two researchers' simultaneous, independent assessments in the field. Groundcover classes reflect dominant ground cover or lack thereof. Classes were each of four invasive grass species, undifferentiated native graminoids and forbs, accumulated dead grass leaves of any species (thatch), accumulated woody plant leaf litter of any species (duff), and exposed soil (bare). Record was made only of canopy directly above a given quadrat, and the identity of the individual providing that canopy was recorded.

Table 1. Summary information on each of the six plots included in this study. "Direct seed" planting method entails the direct broadcast of seed. "Seedlings" entails planting of nursery-raised seedlings in discrow rows. See Figure S2 for a full description of the Rudman02 plot.

Tract	USFWS Plot Code	Planting Year	Survey Year	Plot Age (yr)	Planting Method	Planting and Survey Information					Soil Types Represented				
						Area Planted (ha)	Planting Density (#/ha)	Area Sampled (ha)	Area Sampled (%)	N 1 m^2 Seedling Quadrats	Source for Survey Data	Fine Sandy Loam (%)	Sandy Loam (%)	Sandy Clay Loam (%)	Clay Loam (%)
Sal del Rey	6a	2018	2019	1	Seedlings	1.21	986	1.21	100	—	Mohsin et al. (2021)	87	13	0	0
Sal del Rey	10 fg	2016	2019	3	Seedlings	18.25	986	0.78	4.3	211	This study	99	0	0	1
Sal del Rey	11d	2013	2019	6	Seedlings	18.53	1,444	0.64	3.5	185	This study	81	0	16	3
Sal del Rey	SR80	2006	2020	14	Seedlings	33.40	708	0.77	2.3	313	This study	100	0	0	0
Sal del Rey	SR52	1996	2019	23	Seedlings	9.59	510	0.68	7.1	206	This study	100	0	0	0
Teniente	Rudman02	1987	2020	33	Fallow	10.39	—	0.28	2.7	—	This study	100	0	0	0
Teniente	Rudman30	1987	2020	33	Direct seed	4.32	—	0.28	6.5	—	This study	77	0	22	0

Quantifying Stand Development and Dynamics

We quantified stand development separately for the planted cohort and recruited populations (see Supplement S2) both in terms of the aboveground biomass per unit area (AGB_{area} ; Mg/ha; see below) and abundance (N_{area} ; number of individuals/ha) of woody plants. We discretized the community into size classes based on stem effective diameter at ground height (DGH_{eff} , where for multitemmed individuals, DGH_{eff} is the effective diameter if the sum of the basal area of all individual stems was present in a single stem), and present the number density of individuals for three size classes: DGH_{eff} less than or

equal to 5 cm, 5–20 cm, and greater than 20 cm. We estimated the survival (unitless) of each species as a function of time by dividing the surveyed number density (strictly those we determined which were planted, and not recruited) of each species by the planting density of that species at each plot (see Supplement S3 for a full description).

Because plots were planted at different densities of seedlings, with younger plots reflecting current FWS protocol to plant at approximately 1,000 seedlings/ha (Table 1), we present standardized N_{area} and AGB_{area} (see below) to what would be expected if all plots were planted with a common planting

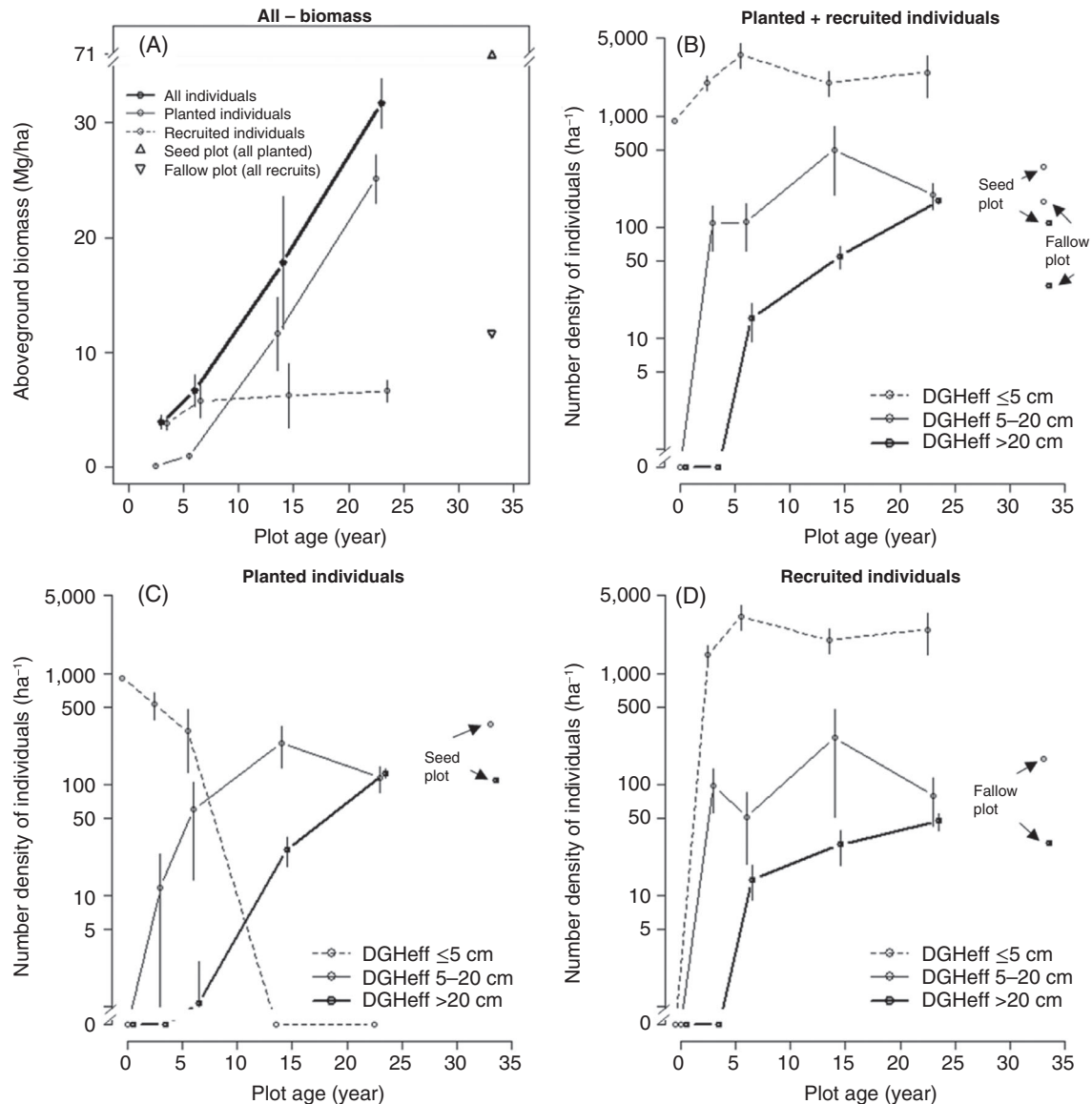


Figure 2. Standardized chronosequence of (A) aboveground biomass (AGB_{area}) and (B)–(D) number density (N_{area}) \pm SE ($n = 8-10$ 10×80 m² subtransects for individuals > 5 cm DGH ; $n = 10-16$ clusters of 20 1×1 m² quadrats for individuals < 5 cm DGH). AGB_{area} and N_{area} are standardized to a planting density of 1,000 individuals per hectare (see the Methods section). Note the difference in legend for (A) and (B)–(D); (A) presents one line each for all individuals, planted and recruited (not planted) populations separately, whereas in (B)–(D) number density contributions are broken down by effective DGH_{eff} size class. The age (x-axis) value of points is offset slightly from each other to aid in visualization where points overlap. The 33-year aged point is represented by two field plots, a direct seeded plot of a single species (*Ebenopsis ebano*) and a fallow plot that has remained mostly unplanted (see Fig. S2).

density of 1,000 seedlings/ha; this applied only surveys of the planted cohort (see Supplement S3 for a full description). For recruits, we only estimated standing recruitment density, not recruitment rate (as this requires repeat observations in time), and we report both the temporal trends in the number density of recruits for the same three size classes as presented for planted individuals, as well as the species-specific mean recruitment density across all plots ($N_{recr,i}$; ha⁻¹).

Biomass Estimation

We estimated the aboveground biomass of individual trees (AGB_{indiv}; kg) using published allometric equations based on stem DGH (cm) and stem height (H ; m) using the equations developed for Tamaulipan thornscrub by N avar et al. (2004) and Rojas-Garcia et al. (2015). Stem height in these equations is perpendicular to the ground (Jose Navar, personal

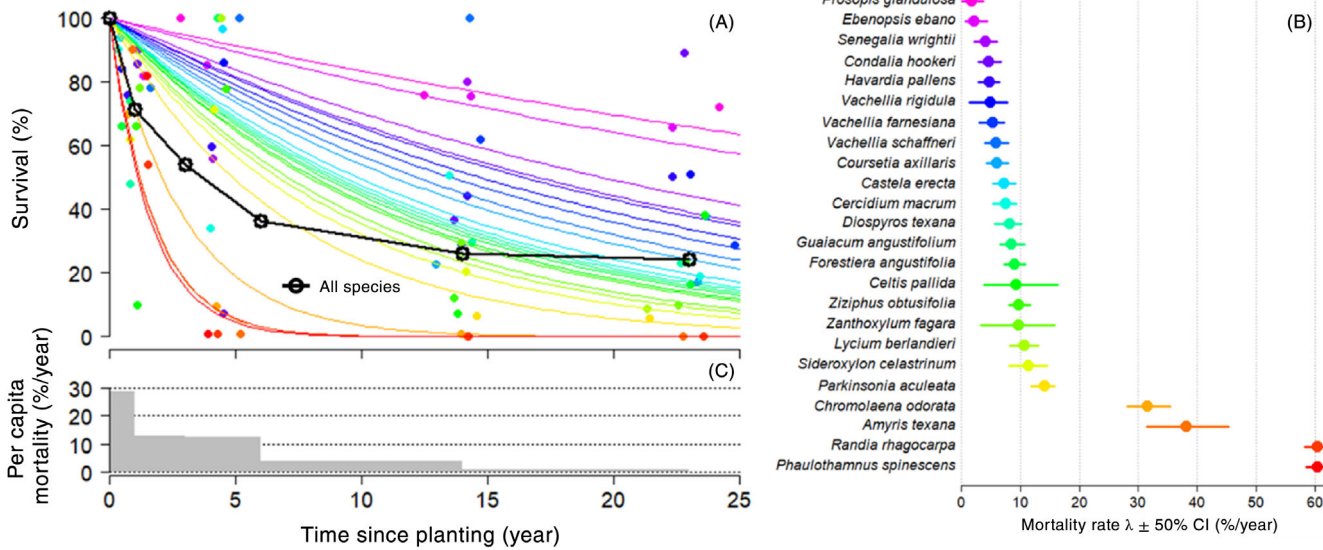


Figure 3. Community and species-specific survival trajectories and associated mortality rates as determined from a chronosequence spanning 1–23 years since planting. (A) Species are ordered and colored cool to warm in terms of increasing mortality rate λ (%/year), shown in (B). (C) Inferred community-level mortality rate m (%/year) in between successive plot ages.

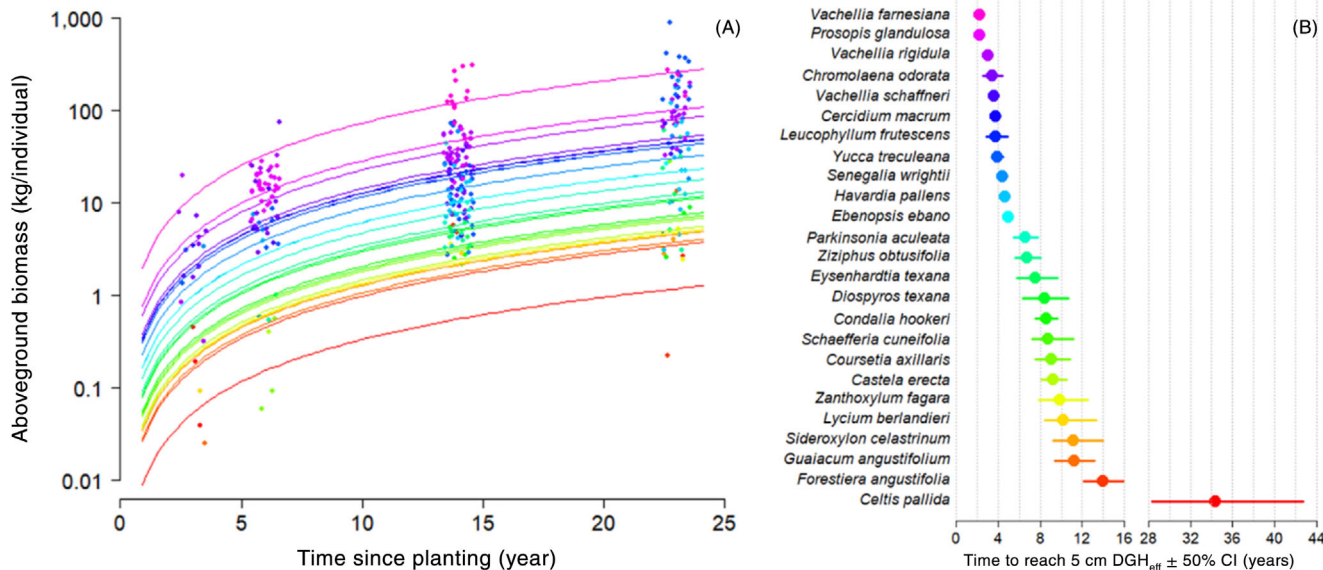


Figure 4. (A) Biomass growth trajectories for planted individuals encountered in at least one plot, fitted to the function $AGB_t \sim GR_{AGB,i} t^\tau$, where GR_{AGB} is the species-specific biomass growth rate and scaling exponent τ is a constant. (B) Species are ordered top to bottom in terms of decreasing growth rate, shown as the time required to attain a basal diameter of 5 cm.

communication). We used R (R Core Team 2019) for all biomass calculations; the full code for which, complete with corrections made (where errors or contradictions existed in the original equations of N avar et al. 2004 or Rojas-Garcia et al. 2015), is given in Supplement S4.

Species-Specific and Community-Level Mortality and Growth Rates

We used the discrete estimates of species survival along the chronosequence together with a statistical model (see Supplement S5 for full description) to estimate species-specific mortality rates (λ_i ; individuals individual⁻¹ yr⁻¹).

To fit the species-specific λ_i s, we log-transformed survival and used a linear mixed model (LMM: lme4 package in R; Bates et al. 2015), forced through the origin, where time was the main effect and species identity was a random slope effect. Only species with planted individuals present in at least two plots were included. We also assessed how the whole-community mortality rate of the planted cohort ($m(t)$; individuals individual⁻¹ yr⁻¹) declined with time (see Supplement S5).

We modeled species-specific aboveground biomass growth rates ($GR_{AGB,i}$; kg/year^t) by fitting a power function to individual aboveground biomass for planted individuals only as a function of plot age.

We first log-transformed both the biomasses and plot ages and used a LMM with time as the main effect and species

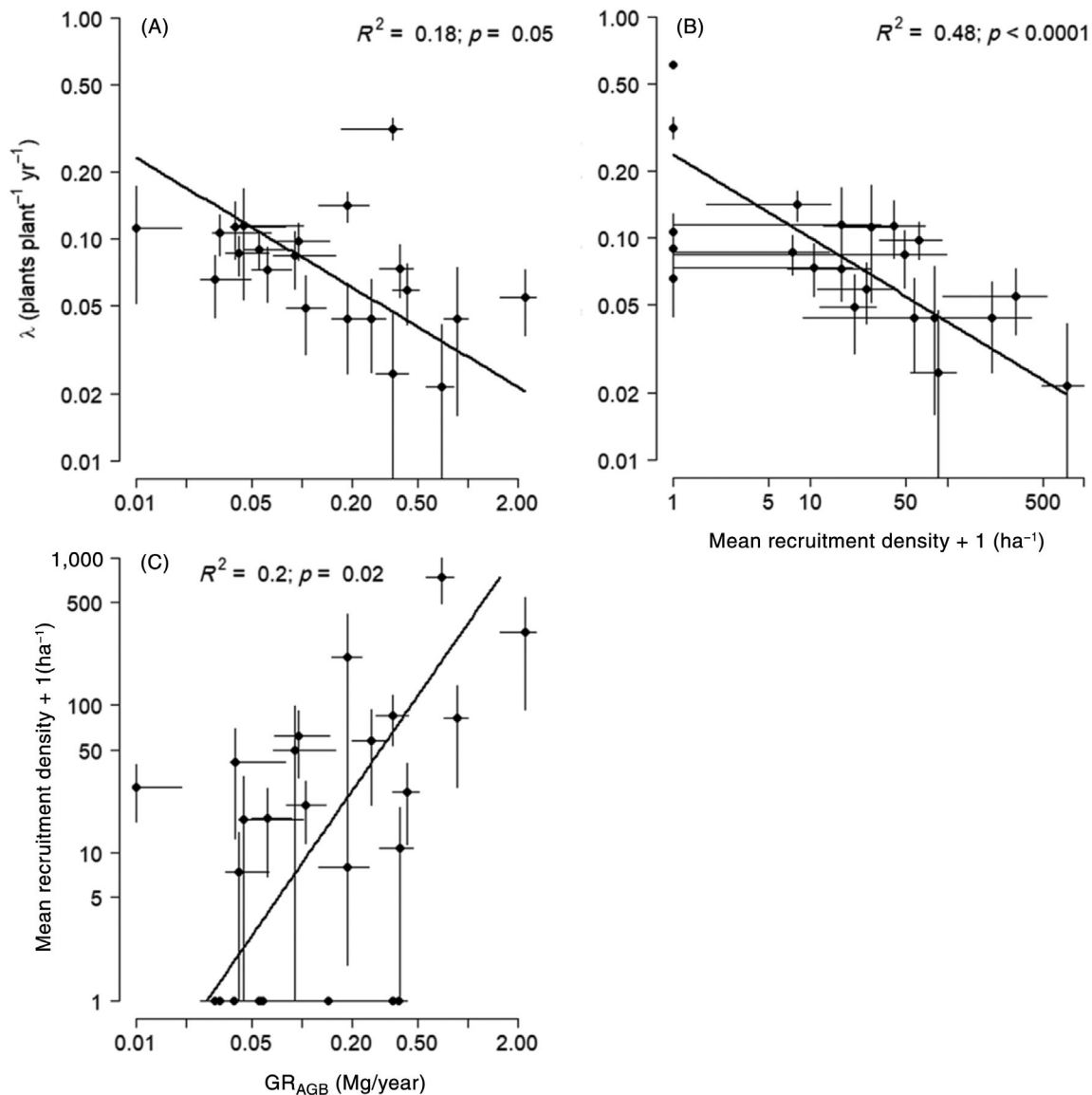


Figure 5. Interspecific relationship between (A) mortality rate λ and aboveground biomass growth rate GR_{AGB} , (B) λ and mean (across $n = 5$ plots) standing density of nonplanted individuals (N_{recr}), and (C) N_{recr} and GR_{AGB} . Error bars indicate $\pm 50\%$ CI for λ and GR_{AGB} and the standard error of mean for N_{recr} . Standardized major axis regression best fit curve is shown.

identity as a random intercept effect, while holding the scaling exponent constant across all species.

Functional Trait Classification

We conducted literature searches for our focal plant species to identify values for a suite of functional traits known to play important roles for plants in semiarid regions: leaf phenology, nitrogen fixation, presence of a photosynthetic stem, rooting depth, and overall stature (Table S3; Richardson & King 2011). For nitrogen fixation, many species included in this study have not been assessed directly, and their categorization is based on assessments of congeners or members of the same family. Degree of uncertainty, in this case, is treated as roughly equivalent to the smallest taxonomic level shared with a species known to fix nitrogen, where a species is categorized as Y (yes) if it has been shown to fix nitrogen, U-L (unknown but likely) if it is in the same genus as a known nitrogen-fixer, U-P (unknown but possible) if it is in the same family or subfamily as a known nitrogen-fixer, U-U (unknown but unlikely) if it is in a family with no known

nitrogen-fixers, and N (no) if it is known definitively to not fix nitrogen. Unassessed species in families from which nitrogen fixation is not known are treated as nonfixing. For rooting depth, we classified species as deep, intermediate, or shallow rooted, even as this classification oversimplifies the array of possible root architectures. For analysis, we collapsed trait values into the most meaningful binary groups and assessed each trait’s effect on species estimates of mortality (λ_i) and growth ($GR_{AGB,i}$) separately using a Wilcoxon rank sum test.

Recruitment Versus Planted Contributions to Species-Specific Biomass Patterns and Trends

We assessed the relative dominance of species on the landscape as well as any detectable temporal trends that would be associated with near-term (5–10 years) changes in dominance. We assessed species dominance using species aboveground biomass per unit area ($AGB_{area,i}$; Mg/ha) for both planted and recruitment contributions, focusing on intermediate-aged plots (15 and 23 years). For temporal trends in dominance, we used linear

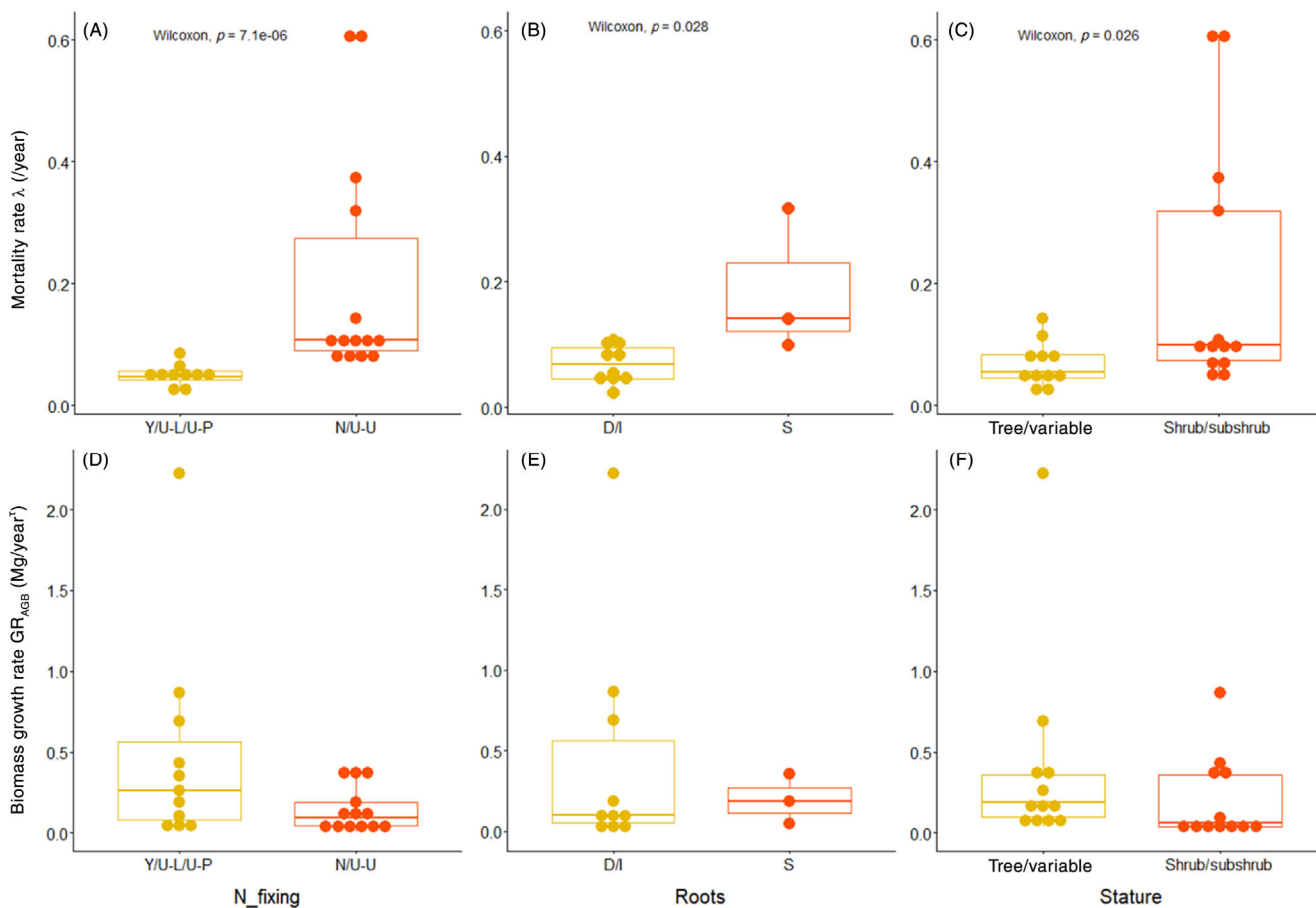


Figure 6. Boxplots of species mortality rate (A)–(C) and biomass growth rate (D)–(F) as given by three functional characteristics: (A, D) nitrogen-fixing ability (Y = yes, U-L = unknown but likely based on genus affiliation, U-P = unknown but possible based on a family or subfamily with a known N-fixer, U-U = unknown but unlikely based on family affiliation, N = no), (B, E) rooting habit (D = deep, I = intermediate, S = shallow), and (C, F) growth form (variable denotes species taking on both tree and shrub forms). p -Values of Wilcoxon rank sum tests are shown where significant at the 0.05 level.

regression of log-transformed $AGB_{area,i}$ (recruited and planted populations separately) for plot ages greater than or equal to 3 years, after standardizing the planted $AGB_{area,i}$ to a common species-specific planting density (see Supplement S3 and Figure S3). We present the biomass growth rate at 23 years (as $dAGB/dt = B0 * GR e^{GR*23}$) for those species with linear trends of $p < 0.15$. We chose a relatively high threshold for significance because we only sampled four discrete ages (3, 6, 14, and 23 years) to detect trends; as such these trends should be interpreted as tentative. $AGB_{area,i}$ for all species (with and without standardization) are given in Tables S6, S7, and S8 for planted, recruited, and all individuals, respectively.

Assessing Impacts of Herbaceous and Woody Canopy Cover on Seedling Abundance

As the vast majority of seedling quadrats did not have seedlings, we used quantile regression with the `quantreg` package in R (Koenker 2020) to detect whether levels of herbaceous cover for certain species or groups influenced the maximum abundance of seedlings at the 1 m² scale. Quantile regression is useful for detecting factors controlling the upper limit of a response when other factors (usually not measured) are limiting. We also assessed

whether presence/absence of woody canopy influenced the abundance of seedlings at this scale, using a Wilcoxon rank-sum test.

Results

In all, we surveyed 5,223 stems of 4,606 individuals across 33 species in seven plots aged 1–33 years (Table S4). Aboveground biomass per unit ground area (AGB_{area}) did not stabilize at 23 years post-planting, increasing at an average rate of 1.41 Mg ha⁻¹ yr⁻¹ over the first 23 years ($p = 0.008$) primarily due to growth of the planted cohort (1.29 Mg ha⁻¹ yr⁻¹; $p = 0.007$), as temporal trends in recruitment biomass accumulation were not significant ($p = 0.17$) (Fig. 2A). The 33 year-old plot with direct broadcast of a low-diversity seed mixture resulted in a monospecific stand of *Ebenopsis ebano* and accumulated aboveground biomass 52% faster (2.15 Mg ha⁻¹ yr⁻¹) than the transplanted seedling plots (Fig. 2A), primarily due to the higher number density of medium-sized individuals (Fig. 2C). In contrast, the 33-year-old fallow plot accumulated aboveground biomass 75% more slowly (0.35 Mg ha⁻¹ yr⁻¹) than the transplanted seedling plots, due to a significantly lower number density of large individuals (Fig. 2B). For both planted and recruited populations, N_{area} of both mature size classes ($DGH_{eff} = 5\text{--}20$ cm and >20 cm) increased with time but the 5–20 cm size class appears to be saturating after 15 years

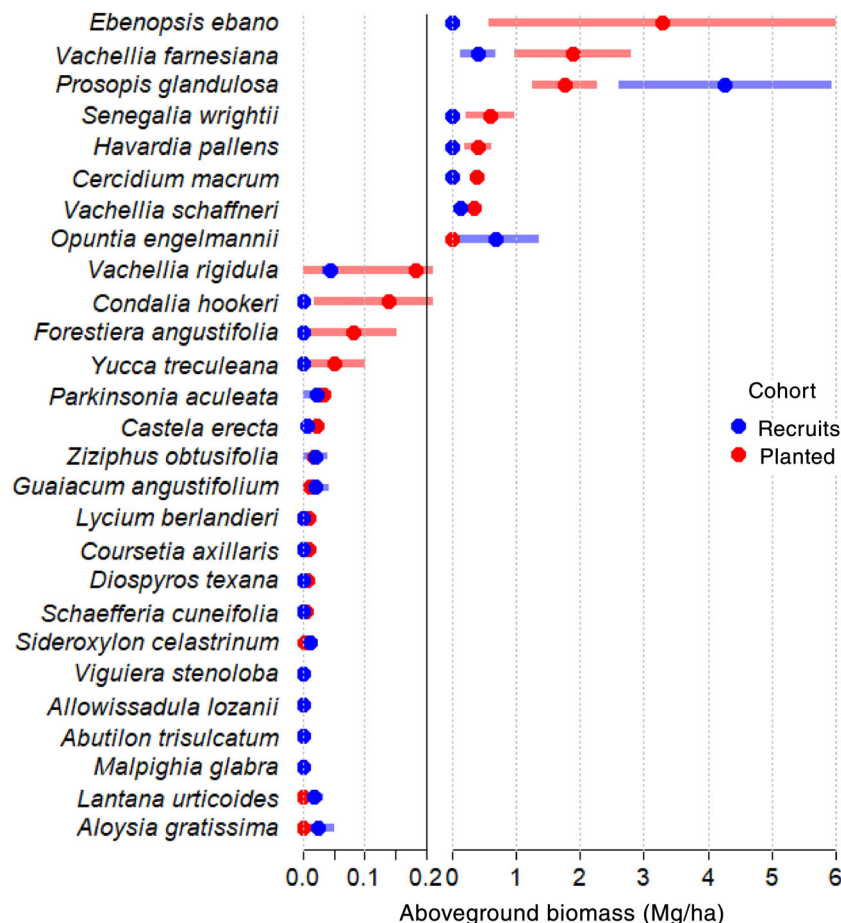


Figure 7. Species-specific biomass density $AGB_{area,i}$ (\pm interquartile range) of two cohorts of individuals (recruits and planted) in intermediate-aged plots (14 and 23 years since planting).

(Fig. 2B). N_{area} of seedlings and saplings ($\text{DGH}_{\text{eff}} \leq 5$ cm) increased rapidly for the first 6 years, and remained stable thereafter, driven by recruitment (Fig. 2B & D). Seedling and sapling N_{area} of the planted cohort fell to zero rapidly with time as expected, as individuals grew into larger size classes (Fig. 2C) or died. N_{area} of both mature size classes increased at a decreasing rate with time for both planted and recruiting cohorts (Fig. 2C & 2D). Although N_{area} of the largest size class ($\text{DGH}_{\text{eff}} > 20$ cm) will likely continue to increase beyond 23 years for the planted cohort (Fig. 2C), the corresponding cohort for the recruited cohort will likely not (Fig. 2D).

Of the 24 species planted and present in at least two plots, we detected a 30-fold range of mortality rates (Fig. 3A & 3B). At the community level, mortality rate was high initially and declined with time (Fig. 3C). Subsequent decreased mortality at the community level reflects higher average survival of those species which survived the seedling stage. *Prosopis glandulosa* and

E. ebano had the lowest mortality rates, with greater than 60% survival 23 years post-planting, while *Randia rhagocarpa* and *Phaulothamnus spinescens* had the greatest mortality (Fig. 3B). Similarly, we observed several orders of magnitude variation in the biomass attained by planted species at 23 years (Fig. 4A), reflective of large variation in species biomass growth rate (GR_{AGB} ; Fig. 4B). The inferred time (years) for species to attain an effective basal stem diameter of 5 cm varied 17-fold (Fig. 4B), with two species requiring as little as 2.1 years (*Vachellia farnesiana*, *P. glandulosa*) and others requiring >10 years (*Sideroxylon celastrinum*, *Guaiaacum angustifolium*, *Forestiera angustifolia*, and *Celtis pallida*).

Species λ declined with increasing GR_{AGB} (Fig. 5A), but with some species having high λ given their moderate to high growth rate (*Chromolaena odorata*, *Parkinsonia aculeata*, and *V. farnesiana*), and others with notably low λ given their low

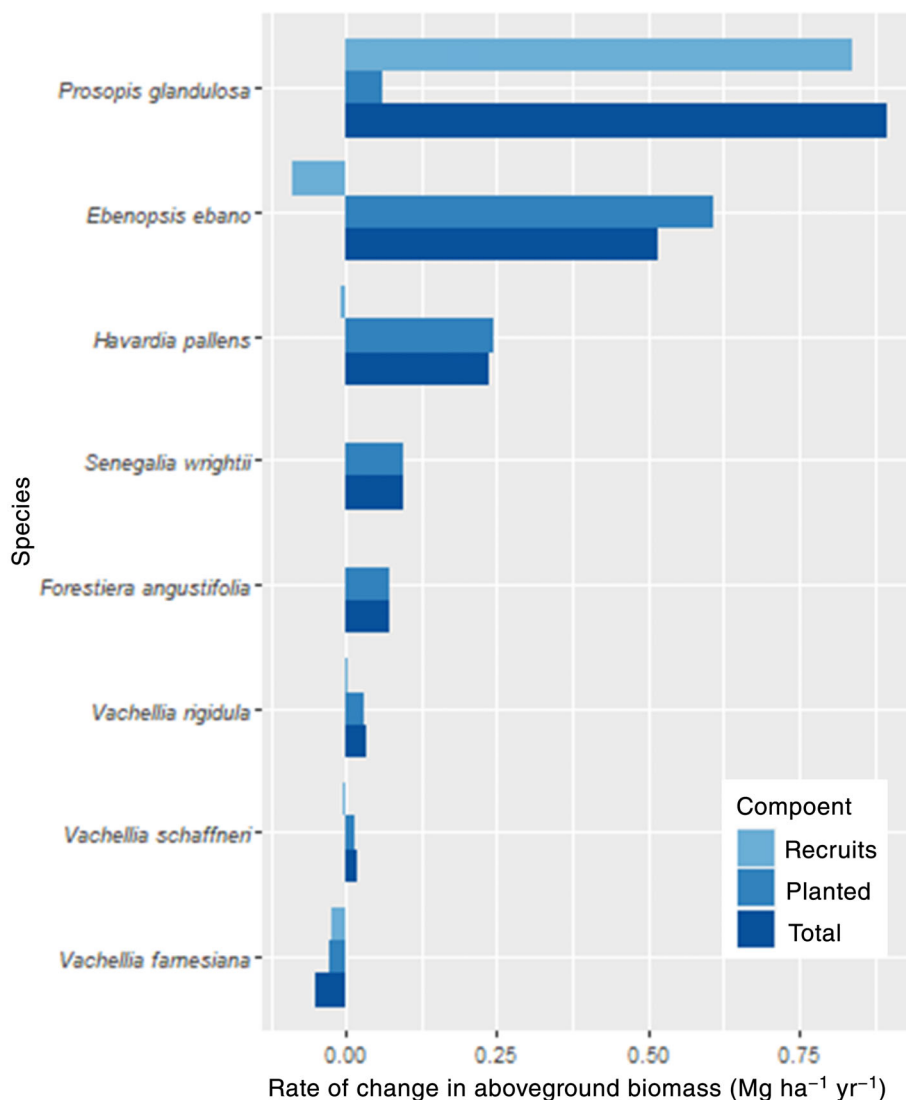


Figure 8. Expected near-term temporal changes in species-specific biomass accumulation at 23 years (total; dark blue bars) and the contribution of the initial planted cohort (medium blue) versus natural recruitment (light blue) to the total change. Species-specific trajectories are given for species present in at least three out of four plots and are based on fits to log-transformed aboveground biomass (Mg/ha) as shown in Figure S4.

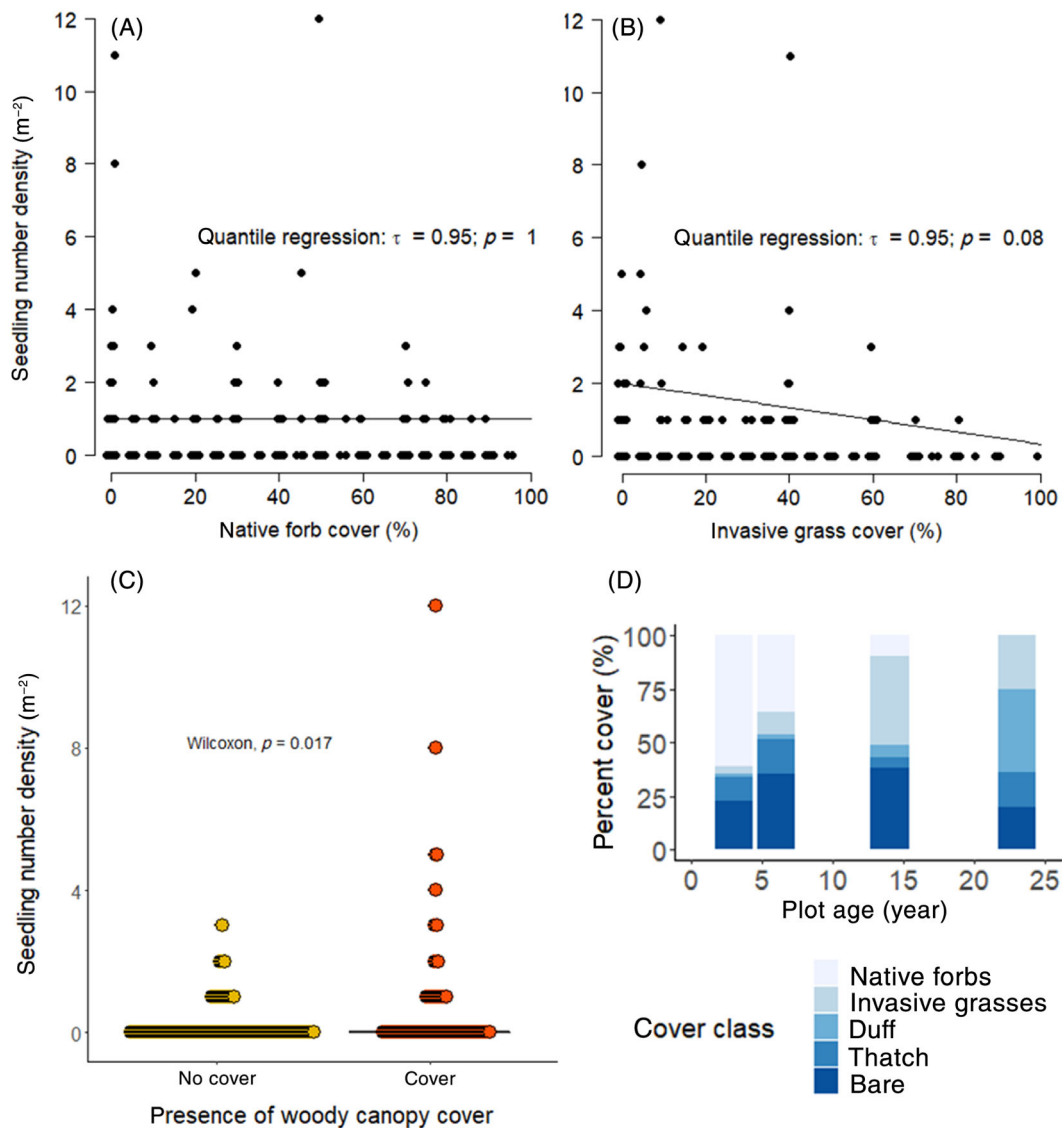


Figure 9. Seedling recruitment in relation to (A) native forb, (B) invasive grass, and (C) woody canopy cover in quadrats with less than 10% invasive species grass cover, and (D) the chronosequence of herbaceous cover. Results of statistical tests are given where significant (or marginally so), else “ns” is shown. Quantile regression in (B) is fit through the upper 95% percentile of points ($\tau = 0.95$).

growth rate (*Coursetia axillaris*, *C. pallida*; Table S5). Species λ also declined strongly with increasing mean number density of recruits (N_{recr}) across all plots, although there was a large range of mortality (6.5–60%) for species not observed to recruit in any plot (Table S5; Fig. 5B). N_{recr} also increased with GR_{AGB} , but with a large range of growth rates for species without any recruits (Fig. 5C).

Mortality was higher in species which do not fix nitrogen (vs. those which are known to or may fix N based on taxonomic affiliation; Fig. 6A), have shallow roots (vs. those which have roots of intermediate or great depth; Fig. 6B), and which attain tree stature (vs. those which are shrubs or subshrubs; Fig. 6C). Leaf habit (deciduous vs. evergreen) and presence of photosynthetic stems did not significantly impact mortality (Wilcoxon rank-sum test, $p > 0.33$).

In contrast, no traits predicted differences in GR_{AGB} (Wilcoxon rank-sum test, $p > 0.12$; Fig. 6D & 6E).

Intermediate-aged plots (15 and 23 years) were dominated by a handful of leguminous trees, where *E. ebano*, *V. farnesiana*, and *P. glandulosa* contributed an overwhelming portion of total plot biomass; the remainder contributed by 24 woody and suffrutescent species (Fig. 7). However, the origin of the trees contributing this biomass varied, with biomass of *E. ebano* and *V. farnesiana* contributed primarily by trees which had been included in the original reforestation, and that of *P. glandulosa* contributed by trees which were in the soil seedbank or were dispersed to the site through natural processes. Species with high (low) AGB_{area} were also present in high (low) number density.

We detected temporal trends in aboveground biomass for eight species, which were varied but mostly increasing except

for *V. farnesiana* (Figs. 8 and S4). With the exception of *P. glandulosa*, all of the expected near-term gains in above-ground biomass on the landscape can be attributed to continued growth of the planted cohort (Fig. 8).

The majority (82%) of 1 m² seedling quadrats had no seedlings. Although the number density of seedlings was not related to native forb cover (Fig. 9A), the upper limit (95th percentile) of seedling abundance declined with invasive grass cover and no seedlings were present in quadrats with >80% invasive grass cover (Fig. 9B). In quadrats with less than 10% invasive grass cover, seedling number density was significantly higher when under a woody species canopy than when in full sun (Fig. 9C). Over the first 15 years, the herbaceous component became dominated by a handful of invasive exotic grasses (Fig. 9D), which were primarily *C. ciliaris* and *Panicum maximum* Jacq. (guinea grass), but *Melinis repens* (Willd.) Zizka (natal grass), *Dichanthium annulatum* (Forssk.) Stapf (Kleberg bluestem), and *Cynodon dactylon* (L.) Pers. (Bermuda grass) were also present.

Discussion

Here, we show that even as reforested areas steadily accumulate biomass over approximately 25 years, the diversity of woody and suffrutescent species declines rapidly with time under the conditions of reforestation as practiced historically in this region, and volunteer individuals are primarily a limited subset of those species which survive from the initial planted cohort. Additionally, an apparent suppression of woody seedling survival by a guild of exotic grasses, as well as a clear increase in coverage of those grasses with time to the exclusion of native forbs and other graminoids, suggests a trend toward increasingly suppressed recruitment of native trees and shrubs. These parallel trends represent major obstacles to the long-term effectiveness of reforestation in the LRGV and overcoming them will require modifications to reforestation methods.

Only a Small Number of N-Fixing, Deep-Rooted Tree Species Persist at Detectable Densities

At these farmed old-field sites, most planted species suffered complete or near-complete mortality: out of 29 species planted in at least 4 plots of different ages, 7 were not present in any plot beyond 3 years, and an additional 8 were only observed in only one plot beyond 3 years. Species which persisted at detectable levels on the landscape beyond 15 years were mostly N-fixing legume trees with a deep rooting habit; these same species (except *Vachellia farnesiana*) are also trending to continued increases in biomass in the near term. A deep rooting habit is likely a covarying trait and may not be directly responsible for enhanced survival at the seedling stage. Understanding mechanisms (e.g. positive plant–plant facilitation) that maintain a higher species diversity in undisturbed thornscrub will provide insight into ways to improve success of non-N-fixing species in restoration, and will be the subject of future work.

Many studies have shown similar patterns of legume success over succession, mostly in the tropics (Gei et al. 2018 and references therein), and studies for semiarid subtropical and

temperate regions have documented that early colonizers of old-fields or woody invaders of grasslands are often N-fixers (Van Auken 2000; Van Auken & Bush 1985; Archer 1989), in addition to being a dominant functional group in undisturbed areas (Sprent & Gehlot 2010). Similar to findings of Van Auken & Bush (1985) in a chronosequence study of succession ca. 300 km to the north, *V. farnesiana* also was the most abundant self-recruiting colonizer in young (<7 years) plots, and rapidly reduced in abundance from 7 to 23 years. While these patterns suggest that soil nitrogen is limiting early during seedling establishment, it remains unknown whether intermediate aged plots remain N-limited, as current composition reflects differential mortality early in development (0–5 years). In some cases, the presence of visible browsing damage on surviving individuals of a species implicates herbivory as a partial or whole cause of decline in that species' number density since planting (C Albrecht personal observation). Both soil elemental analysis and factorial experiments manipulating nutrients and herbivores under nurse canopies could disentangle mechanisms limiting species survival and growth (Prober et al. 2005). Some data exist on the relative browse intensity on species included here (Dick et al. 2016; Arias et al. 2021; Mohsin et al. 2021).

Interestingly, species which exhibit relatively high biomass growth rates also survived post-planting and recruited higher mean densities. It is not clear whether a high biomass growth rate itself underlies survival or if it merely indicates a relatively greater tolerance of the environmental conditions of reforestation as practiced regionally. Rapid growth of aboveground or belowground organs may allow a species to escape competition for light or water with invading forbs and grasses early in post-transplantation establishment. Similarly, rapid height increase may allow survival for the simple reason of reduced opportunity for herbivores as height increases, and/or more of the available browse is mature and therefore not as palatable.

Mortality Rates Among Seedling Transplants Require 7–15 Years to Stabilize

The power of the combined chronosequence-planting approach is that we were able to approximate how mortality rates of the planted cohort changed over time. Background mortality rates for the closest point of comparison in tropical dry forests ranged 1.4–6.9% per year (Imbert & Portecop 2008; Lebrija-Trejos et al. 2010; Suresh et al. 2010), which were levels that were not attained until somewhere between 7 and 15 years in the chronosequence here. This suggests that sustained intervention of transplanted seedlings (of the species mix used here) will be required to improve long-term survival, via restoration interventions such as tree shelters and slow-release moisture within microcatchments (Padilla et al. 2011; Alexander et al. 2016; Dick et al. 2016; Mohsin et al. 2021).

Planted Forests Do Not Yet Appear to Be Self-Sustaining at 25 Years: A Worrisome Trend?

Due to the fact that many mature trees present are those of the initial cohort and are not the product of natural regeneration,

growth and mortality trends will be increasingly influenced by seedling recruitment rates as mature, planted trees begin to senesce. Despite the general trend of increasing recruitment density with declining mortality rate, some species included in these reforestation such as *Ebenopsis ebano* and *Vachellia rigidula* survive and accumulate biomass at a high rate, but under the present conditions only very rarely produce offspring which survive beyond the seedling stage. Hence, it remains possible that some species may begin a rapid decrease in number density and biomass per hectare as individuals begin to senesce without replacements to maintain a stable number density on the landscape.

Moreover, a concerning trend is the increase in abundance of highly competitive invasive grasses and their accumulating thatch, to the exclusion of an initial cover of native forbs and native seedlings. The compositional trend in the herbaceous understory is consistent with the observation that the recruit biomass of every tree species except *Prosopis glandulosa* is stable or decreasing with time. Collectively, these two trends suggest, in a worst-case scenario, that this landscape could transition to an alternate degraded stable state in the coming decades, which can be characteristic of old fields where agriculture was intensive and required substantial fertilization and/or irrigation and few proximate native seed sources exist (Cramer et al. 2008). Similar trends toward limited species diversity and understory recruitment over similar timescales have been observed for restoration plantings using a similarly diverse set of species at a more mesic temperate site in Australia (Munro et al. 2009).

Biomass Accumulation Is Expected to Continue Even as Woody Plant Abundance Stabilizes

We estimate that transplant-based reforestation of approximately 1,000 seedlings/ha at this site contributes substantial native plant biomass after 25 years, adding an additional $1 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ beyond the $0.35 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ that we estimate from natural regeneration alone. Although the number density of large ($\text{DGH}_{\text{eff}} > 20 \text{ cm}$) trees at these sites stabilizes with time, surviving trees continue to grow and accumulate biomass beyond 20–30 years, suggesting that most species which can attain large sizes have done so by 15–20 years, and continued biomass gains will be due to continued growth of the largest trees. Repeat surveys will be required to better estimate the asymptote for aboveground biomass. While to our knowledge no study as of yet has estimated aboveground biomass in remnant undisturbed Tamaulipan thornscrub in the LRGV, in adjacent Nuevo Leon, Mexico, aboveground biomass was 36.75 Mg/ha (Návar et al. 2002), similar to what could be attained here after approximately 25 years with a planting density of 1,000 seedlings/ha. The direct seeded monospecific stand of *E. ebano*, while the greatest in aboveground biomass in this study, also had a high stem density, which has been shown to be associated with a delay in development of tree hollows and fallen coarse woody debris, an important habitat resource (Vesk et al. 2008).

Future Directions

The data reported here identify clear avenues of research relevant to increasing the effectiveness of reforestation in the LRGV

and other semiarid regions. Two major challenges to reforestation are seen: an initial, rapid decline in species diversity post-planting and an apparently depressed recruitment rate in mature forests associated in time and space with increasing coverage of the landscape in multiple invasive grass species. Further research is needed for a robust classification system of species' regeneration niches as related to those site characteristics which can be reasonably modified at the scale of regional reforestation (Grubb 1977; Butterfield & Briggs 2011). Quantification of any of those traits, as well as light-response traits such as light-saturated photosynthetic rate and leaf heat tolerances, may allow species to be placed on a simple scale of preference for sun or shade used to inform staggered plantings or use of restoration technology (Padilla et al. 2009). Additionally, a greater focus on the establishment of native grasses and forbs will likely yield marked improvement in restoration of areas at savanna-forest boundaries (Prober et al. 2005; Buisson et al. 2020).

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Scale diagram of 20 m of transect.

Figure S2. Determination of RUDMAN02 as a mostly fallow plot beginning in 1987.

Figure S3. Observed chronosequence of aboveground biomass (non-standardized for differences in initial planting density).

Figure S4. Species-specific temporal trends of area-based standardized aboveground biomass (Mg/ha) of all (a), planted (b), and recruited (c) individuals.

Table S1. Species planting densities (number planted/ha), with total number of individuals planted in parentheses, across the five Sal del Rey plots where planting information was known.

Table S2. Geographic characteristics of each transect included in this study.

Table S3. Species functional traits as determined from the literature (leaf habit, N-fixing ability, root depth, and stature) and personal observations (photosynthetic stem).

Table S4. Number density (number ha⁻¹) of individuals surveyed (total number recorded in parentheses) in each of seven plots at Sal del Rey and Teniente tracts.

Table S5. Species per capita mortality rate (λ ; yr⁻¹) and 50% CI, aboveground biomass growth rate (GR_{AGB} kg/yr^{1.5}) and 50% CI, and the species-specific mean number density of recruits across all plots ($N_{recr,i}$ ha⁻¹) with the standard error range.

Table S6. Species-specific biomass density (AGB_{area,i}; Mg/ha) of planted individuals, both nonstandardized (NonStd) and standardized (Std) to a common species-specific planting across all plots (see the Methods section).

Table S7. Species-specific biomass density (Mg/ha) of recruited individuals.

Table S8. Species-specific biomass density (Mg/ha) of all (planted and recruited) individuals, with the planted contribution both nonstandardized (NonStd) and standardized (Std) to a common species-specific planting across all plots (see the Methods section).

Supplement S1. Physiographic context and reforestation history and methods.

Supplement S2. Distinguishing planted vs. recruited individuals to estimate survival with time.

Supplement S3. Quantifying species-specific survival and standardizing observed number - densities and biomass to a common planting density.

Supplement S4. R code for estimating tree-level biomass (kg dry mass) as a function of height (m) and basal diameter at ground height (cm), following the equations of Navar et al. (2004) and Rojas-García et al. (2014).

Supplement S5. Estimating species-specific mortality rates (λ_i) and time-varying community-level per capita mortality rate $m(t)$.

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